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Upper Ordovician Ecology of the Central Appalachians

Peter William Bretsky, Jr.

Bulletin 34

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Upper Ordovician Ecology of the Central Appalachians

PETER WILLIAM BRETSKY, JR.

Department of Geology
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UPPER ORDOVICIAN ECOLOGY OF THE CENTRAL APPALACHIANS

BY PETER WILLIAM BRETSKY, JR.

ABSTRACT

The upper Reedsville Formation and portions of equivalent Martinsburg strata (Upper Ordovician) in the central Appalachians provide one of the earliest known examples of a prolific clastic-facies invertebrate fauna with a distinctly modern aspect. This study is a paleoecological investigation of the faunal communities comprising this invertebrate assemblage (especially the classical *Orthorhynchula* Zone of Bassler), and their geographic variation along a 600-mile-long Late Ordovician shoreline. In addition a systematic description of the invertebrates collected during the present investigation was undertaken.

About 5,100 specimens from 164 fossiliferous central Appalachian exposures provided the basis for the description of 31 species (and/or genera) that are most common in this Late Ordovician assemblage. Numerically dominant taxa are the trepostomatous bryozoans, brachiopods, gastropods and bivalve molluscs. The distributional pattern of species within each of these four major taxonomic groups outlines twelve faunal provinces, which are taxonomically distinct enough to aid in more detailed autecological interpretations of the Late Ordovician species.

The zoogeographic and autecological data are combined into a synecological review of the main environmental settings and associated faunas. Those species which show a high degree of affinity and a pronounced tendency to recur together throughout the Upper Ordovician strata are called communities. There are three communities which are further subdivided into seven multi-species populations that are more restricted geographically and stratigraphically, and presumably reflect more localized environmental conditions. The communities and populations are:

(1) *Sowerbyella–Onniella* Community (Strophomenid and Orthid–Crinoid Populations): lived on muddy silt bottoms of the outer sublittoral from central Pennsylvania to north-central Virginia; abundant strophomenid (*Sowerbyella, Rafinesquina*) and dalmanellid (*Onniella*) brachiopods, pleurotomariid gastropods [*Loxoplocus* (*Lophospira*) and *Ruedemannia*], nuculoid (*Ctenodonta*?, *Praenucula*) and actinodontoid (*Lyrodesma*) bivalves, crinoids and lesser numbers of trilobites.

(2) *Orthorhynchula–Ambonychia* Community (Linguloid, Rhynchonellid and Modiolopsid Populations): lived on sand-silt bottoms of the inner sublittoral and intertidal from south-central Pennsylvania to south-central Virginia; abundant rhyn-

chonellid (*Orthorhynchula*) and linguloid (*Lingula*?) brachiopods, bellerophontid gastropods (*Plectonotus*?, *Bucania*), modiomorphid (*Modiolopsis*, *Ischyrodonta*), ambonychiid (*Ambonychia*) and nuculoid (*Tancrediopsis*) bivalves.

(3) *Zygospira–Hebertella* Community (Spiriferid and Orthid Populations); lived on mud and silty mud bottoms of the inner and outer sublittoral from southwestern Virginia to northern Tennessee; abundant spiriferid (*Zygospira*) and orthid (*Hebertella*) brachiopods, pterioid bivalves [*Pterinea* (*Caritodens*)], murchisoniid gastropods (*Murchisonia*), and trepostomatous bryozoans (*Hallopora*, *Dekayia*, *Monticulipora*, *Amplexopora*, *Batostomella*).

This study has shown that the Upper Ordovician rocks in the central Appalachians enclose a shallow water marine fauna that exhibits not only a distinctive onshore to offshore distributional pattern but also a longshore one. Nearshore environments are commonly dominated by bellerophontid gastropods, nuculoid and modiomorphid bivalve molluscs, linguloid and rhynchonellid brachiopods, whereas the offshore regimes are composed predominantly of orthid, strophomenid and spiriferid brachiopods, crinoids and trepostomatous bryozoans. This general distributional pattern is modified significantly by the position of the major source area in central Pennsylvania as the characteristic offshore brachiopods and bryozoans come to occupy more nearshore environments in southwestern Virginia and northern Tennessee.

ZUSAMMENFASSUNG

Die obere Reedsville Formation und Teile der äquivalenten Martinsburg Strata (Obere Ordovizian) in den Zentral Appalachen liefern eine der frühesten bekannten Beispiele einer reichen "clastic-facies" wirbellosen Fauna mit einem ausgeprägten modernen Aussehen. Dieses Studium ist eine paläeökologische Erforschung der Tiergemeinschaften, die diese wirbellose Sammlung (hauptsächlich die klassische *Orthorhynchula* Zone von Bassler) und seiner geographischen Verschiedenheit entlang einer 600-Meilen späten Ordovizian Küste umfassen. Zusätzlich wurde eine systematische Beschreibung von wirbellosen Tieren unternommen, die während der vorliegenden Untersuchung gesammelt wurde.

Ungefähr 5, 100 Proben von 164 fossilienführenden Aufschlüssen in den Zentral Appalachen liefern die Basis für die Beschreibung von 31 Arten (und/oder Gattungen) die am häufigsten in dieser späten Ordovician Sammlung auftauchen. Zahlenmäzige vorherrschende Taxa sind die trepostomatischen Bryozoen, Brachiopoden, Gastropoden und Muscheln. Die Verbreitungsformen der Arten innerhalb jeder dieser vier Hauptgliederungen begrenzen zwölf Tiergebiete. Diese Tiergebiete sind genügend taxonomisch verschieden um ausfuhrlichere autökologische Darstellungen der späten Ordovizian Arten zuzufügen.

Die zoogeographische und autökologische Angaben sind mit einem Uberblick über die hauptsächlichen Milieus und den dazugehörigen Tierwelten verbunden. Die Arten welche einen hohen Grad von Verbindungsfähigkeit zeigen und eine ausgesprochene Tendenz haben zusammen in der Oberen Ordovizian Strata aufzutreten, werden als Gemeinschaften bezeichnet. Es gibt drei Gemeinschaften welche man noch in sieben "multi-species" Populationen welche geographisch und stratigraphisch mehr begrenzt sind und voraussichtlich mehr örtliche Umgebungs-bedingungen aufzeigen. Die Gemeinschaften und Population sind:

(1) *Sowerbyella – Onniella* Gemeinschaft (Strophomenid und Orthid-Krinoid Population): lebte auf schlammigem Böden der äusseren Sublittoralzone von Zentral Pennsylvania bis Nord-Zentral Virginia; zahlreiche strophomenid (*Sowerbyella, Rafinesquina*) und dalmanellid (*Onniella*) Brachiopoden, pleurotomariid Gastropoden [*Loxoplocus* (*Lophospira*)] und *Ruedemannia*, nuculoid (*Ctenodonta*?, *Praenucula*) und actinodontoid (*Lyrodesma*) Muscheln, Krinoiden und weniger Trilobiten.

(2) *Orthorhynchula – Ambonychia* Gemeinschaft (Linguloid, Rhynchonellid und Modiolopsid Population): lebte auf sand-schlammigen Boden der inneren Sublittoralzone und Zwischengezeitenzone von Süd-Zentral Pennsylvania bis Süd-Zentral Virginia; zahlreiche rhynchonellid (*Orthorhynchula*) und linguloid (*Lingula*?) Brachiopoden, bellerophontid Gastropoden (*Plectonotus*?, *Bucania*), modiomorphid (*Modiolopsis, Ischyrodonta*), ambonychiid (*Ambonychia*) und nuculoid (*Tancrediopsis*) Muscheln.

(3) *Zygospira – Hebertella* Gemeinschaft (Spiriferid und Orthid Population): lebte auf schlammigem Boden der inneren und äusseren Sublittoralzone von

Südwest Virginia bis Nord Tennessee; zahlreiche spiriferid (*Zygospira*) und orthid (*Hebertella*) Brachiopoden, pterioid Muscheln [*Pterinea* (*Caritodens*)], murchisoniid Gastropoden (*Murchisonia*), und trepostomatischen Bryozoen (*Hallopora, Dekayia, Monticulipora, Amplexopora, Batostomella*).

Diese Studium hat zezeigt, dass die obere Ordovizian Steine in den Zentral Appalachen eine Flachwasser marine Fauna enthalten, welche nicht nur eine ausgeprägte nahe an der Küste gelegene bis Küste eutfernte Verteilungsform haben, aber auch eine Küste-parallel Form. Nahe an der Küste gelegene Gebiete sind normalerweise beherrscht von bellerophontid Gastropoden, nuculoid und modiomorphid Muscheln, linguloid und rhynchonellid Brachiopoden, während die von der Küste entfernten Gruppen sind vorherrschend von orthid, strophomenid und spiriferid Brachiopoden, Krinoiden und trepostomatsche Bryozoen zusammengesetzt. Diese allgemeine Verteilungsform is bedeutend verändert von der Lage der Hauptlieferungsgebiete in Zentral Pennsylvania als die bezeichnenden vom Lande eutfernte Brachiopoden und Bryozoen begannen näher an der Küste gelegenen Gebiete in Sudwest Virginia und Nord Tennessee zu besetzen.

РЕЗЮМЕ

Верхняя часть формации Ридсвил (Reedsville) и некоторые части соответствующих этой верхней части по возрасту Мартинсбергских (Martinsburg) слоев (верхний ордовик), в центральных Аппалачах, содержат один из самых ранних примеров богатой фауны беспозвоночных кластической фации и отчетливо современного вида. Предлагаемая работа — результат палеоэкологического исследования фаунальных обществ, включающих эту ассоциацию беспозвоночных (в особенности, классическую зону с *Orthorhynchula* Басслера) и их географических изменений вдоль поздно-ордовикского берега, длиной в 1000 километров. Кроме того, беспозвоночные, собранные в течение наших исследований, систематически описаны.

Около 5100 экземпляров из 164 фоссилоносных выходов в центральных Аппалачах служили базисом для описания 31 самых распространенных в этой поздно ордовикской ассоциации видов и родов. Численно преобладающие таксоны — трепостоматные мшанки, брахиоподы, брюхоногие и двустворчатые моллюски. Распределения видов этих четырех таксономических групп определяют двенадцать фаунальных провинций, которые таксономически различаются в достаточной степени, чтобы оказались полезным для детальной автоэкологической интерпретации поздно ордовикских видов.

Зоогеографические и автоэкологические данные объединены в синэкологический обзор главных типов сред и ассоциированных с ними фаун. Группы видов, показывающих в высокой степени склонность проявляться вместе снова и снова в течение отложения верхне-ордовикских слоев, названы нами обществами. Имеются три общества. Они подразделены в семь многовидных популяций, более ограниченных географически и стратиграфически, и предположительно, соответствующих более локализованным условиям среды. Общества и популяции:

(1) Общество *Sowerbyella-Onniella* (строфоменидная и ортидо-криноидная популяция), которое жило на илистом дне внешнего сублиторала, от центральной Пенсильвании до северо-центральной Вирджинии: обильные строфоменидные (*Sowerbuella, Rafinesquina*) и далманеллидные (*Onniella*) брахиоподы, плеуротомариидные брюхоногие [*Loxoplocus* (*Loxospira*)] и *Ruedemannia*, нукулоидные (*Ctenodonta?, Praenucula*) и актинодонтоидные (*Lyrodesma*) двустворчатые, криноиды и менее число трилобитов.

(2) Общество *Orthorhynchula-Ambonychia* (лингулоидная, ринхонеллидная и модиолопсидная популяция), которое жило на песчано-иловых днах внутреннего сублиттораля и зоны прилива, от юго-центральной Пенсильвании до юго-центральной Вирджинии: обильные ринхонеллидные *(Orthorhynchula)* и лингулоидные *(Lingula ?)* брахиоподы, беллерофонтидные брюхоногие *(Plectonotus ?, Bucania)*, модиоморфидные *(Modiolopsis, Ischyrodonta)*, амбонихиидные *(Ambonychia)* и нукулоидные *(Tancrediopsis)* двустворчатые.

(3) Общество *Zygospira-Hebertella* (спириферидная и ортидная популяция), которое жило на иловых днах внутреннего и внешнего сублиттораля, от юго-восточной Вирджинии до северного Теннесси: обильные спириферидные *(Zygospira)* и ортидные *(Hebertella)* брахиоподы, птериоидные двустворчатые [*Pterinea (Caritodens)*], мурчисониидные брюхоногие *(Murchisonia)* и трепостоматные мшанки (*Hallopora, Dekayia, Monticulipora, Amplexopora, Batostomella*).

Наши исследования показали, что верхне-ордовикские породы в центральных Аппалачах заключают мелководную фауну, обнаруживающую характерное распределение, которое варьирует не только с удалением от берега, а тоже с смещением вдоль берега. В прибрежных средах обычно доминируют беллерофонтидные брюхоногие, нукулоидные и модиоморфидные двустворчатые моллюски, лингулоидные и ринхонеллидные брахиоподы, тогда как у режимов открытого моря преобладают ортидные, строфоменидные и спириферидные брахиоподы, криноиды и трепостоматные мшанки. Это общее распределение, замечаемое в главной области собирания в центральной Пенсильвании, значительно изменяется вдоль древнего берега: характерные брахиоподы и мшанки открытого моря находятся в средах, близких берегу, в юго-западной Вирджинии и северном Теннесси.

INTRODUCTION

The present work is a paleoecologic study and systematic redescription of the invertebrate faunas, especially the *Orthorhynchula* Zone fauna, from the fossiliferous beds at the top of the Reedsville Formation (Upper Ordovician) in the central Appalachian Valley and Ridge Province. Also included in this study are data from the Shochary Sandstone Member of the Martinsburg Formation in the Great Valley of eastern Pennsylvania (see Bretsky et al., 1969). The investigation was undertaken because these Lower Paleozoic rocks preserve the first major incursion of a clastic-facies invertebrate fauna in Paleozoic rocks of the Appalachians. Earlier Paleozoic faunas in the Appalachian region occur predominantly in carbonate rocks. The fossil assemblage is especially significant because it is the earliest to contain recognizable nearshore faunas of distinctly modern aspect.

Only a few workers on Paleozoic invertebrates have stressed the ecology of clastic-facies faunas. The preliminary studies of Ziegler (1965) in the British Silurian and of Sutton et al. (1966) in the New York Devonian are illuminating contributions, as are the investigations of Elias (1937), Johnson (1962) and Stevens (1966), principally in the Mid-Continent Pennsylvanian and Permian.

This investigation is concerned with the faunal associations and their zoogeographic variations along the Reedsville-Martinsburg outcrop belt that extends from northeastern Pennsylvania to northern Tennessee (Fig. 1). It includes Bassler's (1919) *Orthorhynchula* Bed or Zone. The zone was named for an abundant species of rhynchonellid brachiopod, *Orthorhynchula linneyi* (James), which Butts (1940, p. 208) had found "universally present and abundant in the *Orthorhynchula* Bed from central Pennsylvania to the south end of Clinch Mountain . . . Tennessee." The zone, however, is characterized by inarticulate as well as rhynchonellid brachiopods, gastropods, bivalve molluscs and trepostomatous bryozoans, not all of which are found at every exposure of the "zone" in the central Appalachians. Furthermore, *Orthorhynchula linneyi* occurs in Middle and Upper Ordovician rocks in central Tennessee and Kentucky (Wilson, 1949; Foerste, 1910), but earlier investigators stressed the broad biostratigraphic importance of the *Orthorhynchula* Zone fauna specifically along the Appalachian Valley and Ridge Province. The *Orthorhynchula* Zone has been inter-

preted as a marker bed that has little or no time significance, but rather is integrally related to a particular lithology (Woodward, 1951, p. 335 ff.; Butts, 1945, p. 5). Butts (1940, p. 208) states that the rock type is a "slightly calcareous, generally fine-grained . . . thick or massively bedded sandstone". A few pages later, however, he (1940, p. 217) says that the *Orthorhynchula* faunas were found preserved in a variety of limestones, shales and sandstones; therefore, the zone may also have been viewed as a local range zone or teilzone, although this interpretation has never been stressed in the earlier literature. Also the paleogeographic relationships of these zonal faunal elements to other abundant Upper Ordovician faunas in the Appalachians were never clearly defined, and because I have emphasized the environmental aspects of this fauna, I would thus prefer to view the *Orthorhynchula* Zone as a fossil community zone (see Berry, 1966, p. 1492).

The stratigraphic range of this zone at the top of the Reedsville Formation was determined by the maximum thickness of the beds containing the *Orthorhynchula* assemblage in central Virginia, south-central Pennsylvania and east-central West Virginia (Fig. 2); this normally amounted to about 100 feet or less. The replacement of many of the typical *Orthorhynchula* Zone fossils in this stratigraphic interval by other species and fossil assemblages was determined by a study of closely spaced sections along the out-crop belt from northeastern Pennsylvania to northern Tennessee.

State and regional geologic maps provided the stratigraphic base for the study. The surveys of Butts (1933), Cloos (1941), Rodgers (1953), Stose (1932), Gray (1960) and Calver (1963) were supplemented by a number of quadrangle reports dealing with north-central Virginia and southern Pennsylvania. Other central Appalachian literature was surveyed for reference to any previously known exposures of fossiliferous Upper Ordovician rocks. Many of these previously published stratigraphic sections were adequate only in so far as they gave some indication of the overall thickness of the fossiliferous upper Reedsville strata. The total number of localities visited amounted to more than 200, but fossils were present and collected from only 164. About 5,100 specimens from these 164 fossiliferous exposures provided the basis for the description of 31 species (and/or genera) that are incorporated into a systematics section at the end of this paper. At over 90 localities fossils were collected from well-defined stratigraphic horizons, approximately 35 additional localities served, to some degree, as accurate stratigraphic control; the remaining 40 localities were of more limited value, for the exact order and thickness of the various rock units were not clear at these exposures. In this study data were gathered concerning bedding features, lithologic type and relative abundance of species. Tentative field identifications of both rock and fossil materials were checked in the laboratory.

Grain size of terrigenous material accords with the Wentworth grade scale (1922). Bedding thickness is classified after McKee and Weir (1953) and Ingram (1954). The textural classification of detrital rocks generally follows the one presented by Krumbein and Sloss (1963, p. 153). Bathymetric terms are used in the reconstruction of these Paleozoic environmental settings, and the reader is cautioned to view these only as reasonable estimates. Hedgpeth (1957, fig. 1) and Valentine (1961, fig. 2) diagram and briefly discuss the use of the terms, "littoral, and inner and outer sublittoral", all of which refer to the shelf environments in water of less than 200 meters depth. The synecological terms frequently used in this paper are:

Community—An association of recurring species that are numerically dominant and show some relationship to a physical environment or environmental parameter. This definition applies to the organism and habitat communities of Newell et al. (1959) and agrees with the definitions of marine level-bottom communities given by most marine biologists (see Speden, 1966).

Population—All the organisms presumably inhabiting an area during any given

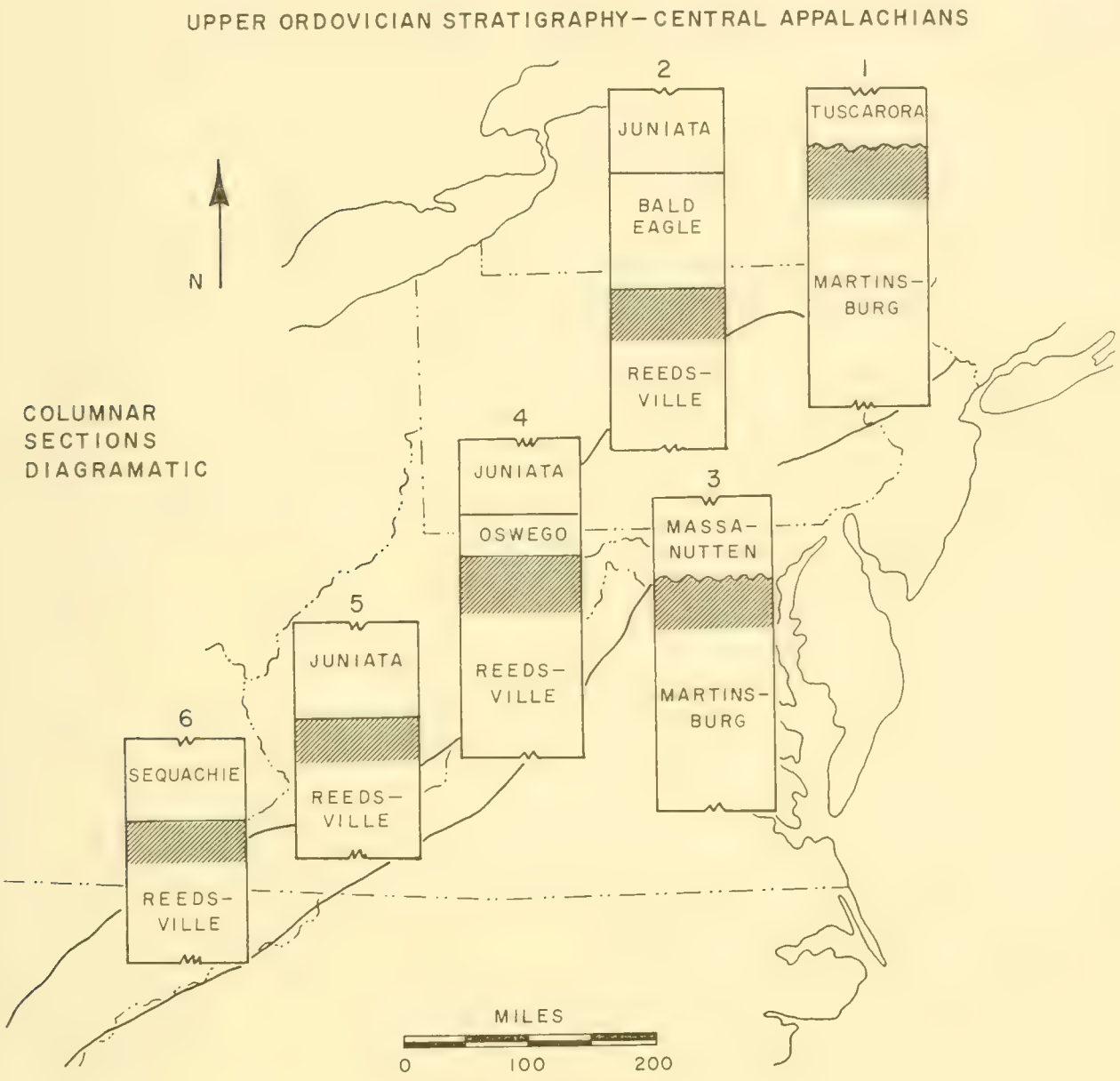

FIG. 2. Schematic columnar sections, Upper Ordovician strata north-central Appalachians. Data primarily from Twenhofel et al. 1954. Cross-hatched area of each column indicates fossiliferous rocks studied in this report. Outline of Valley and Ridge Province shown as solid lines from Pennsylvania into Tennessee.

Location of sections:

1. Eastern Pennsylvania, Shochary Ridge
2. South-central Pennsylvania
3. Northern Virginia, Massanutten Mountain
4. Eastern West Virginia and west-central Virginia
5. South-central Virginia
6. Northern Tennessee and southwestern Virginia

time—in this case, all those inhabiting some part of the central Appalachians during some interval of the Late Ordovician. As defined by Clarke (1954, p. 333), these may be single-species or multi-species populations. Communities and populations are similarly defined but the latter are more restricted geographically and stratigraphically.

Faunal Province—A geographic region in which a particular systematically segregated taxonomic group maintains a characteristic specific composition (see Valentine, 1961, p. 341, and A.G.I. Glossary of Geology, 1960, p. 106). An example is the central Appalachian Late Ordovician brachiopod fauna, which consists of three distinct faunal provinces, each one dominated by a particular assemblage of brachiopod species.

ACKNOWLEDGMENTS

I am indebted to many individuals for discussion, suggestions and advice during the course of this investigation. Those most actively involved were Dr. Richard Boardman of the U. S. National Museum; Drs. John Pojeta and Ellis Yochelson of the U. S. Geological Survey; and Drs. Karl Waage and Donald C. Rhoads of Yale University. Because I had expressed an interest in studying the zoogeography and ecology of an Early Palezoic fossil assemblage, Dr. A. Lee McAlester suggested the possibility of applying a synecological approach to the classical "*Orthorhynchula* Zone" faunas in the central Appalachians. I sincerely appreciate his continual support and encouragement throughout the investigation.

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STRATIGRAPHIC FRAMEWORK

The paleoecologic reconstruction of the Late Ordovician invertebrate faunas in the central Appalachians involves only those fossiliferous beds at the top of the Reedsville and Martinsburg Formations, specifically the faunas of the classical *Orthorhynchula* Zone or Bed of Bassler (1919). Stratigraphic and geographic relationships are presented in Figure 2 (data primarily from Twenhofel et al., 1954, also see Bretsky, 1969).

The nomenclatural problems surrounding the use of the terms Reedsville Formation, Reedsville lithofacies, Martinsburg Formation and Martinsburg lithofacies are reviewed by McBride (1960, 1962). Ulrich (1911, pl. 27; 1913, p. 644) assigned the term Reedsville Formulation to the fossiliferous Upper Ordovician sandstones and shales in the central Pennsylvania Valley and Ridge Province, to differentiate them from the relatively unfossiliferous Martinsburg Formulation in the Great Valley of eastern Pennsylvania. Figure 3 (modified from Ulrich) presents the correlation of these rock units. Ulrich excluded from the Reedsville some of the underlying Trenton

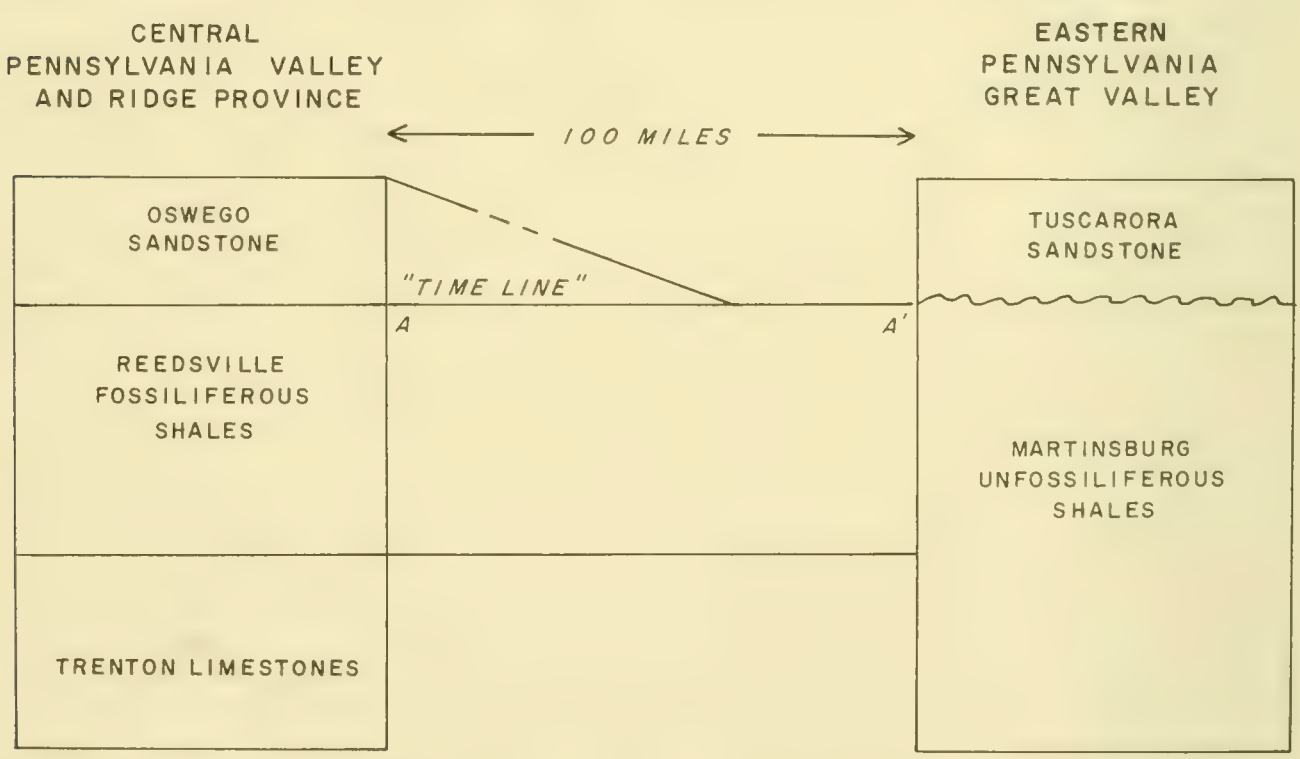


FIG. 3. Correlation of the Upper Ordovician strata in Pennsylvania after Ulrich (1911). The distance between the generalized columnar sections is approximate. The Martinsburg Formation is not totally unfossiliferous (e.g., Shochary Ridge Sandstone Member) but in comparison with the Reedsville Formation it has been referred to commonly as an unfossiliferous shale. Line A-A' connects lithologic units of supposed equivalent age.

limestones which he believed to be equivalent in age to the lowest units of the Martinsburg Formation. The definition of the Reedsville-Martinsburg boundary has, however, lacked precision since Ulrich's differentiation.

McBride (1960, p. 26–27) has interpreted the Reedsville and Martinsburg rocks as lithofacies of each other, with an axis of intersection between these two lithofacies along the western edge of the Great Valley in Pennsylvania and Maryland (Fig. 4). According to his scheme, much of the Martinsburg "barren" shales had been deposited prior to the deposition of the Reedsville fossiliferous shales. In accepting McBride's interpretation I have considered only the Shochary Sandstone beds in eastern Pennsylvania and the fossiliferous siltstones and shales underlying the Massanutten Sandstone in north-central Virginia as part of the Martinsburg Formation. Woodward (1951, p. 332–376) and McBride (1960, p. 12–24, esp. table 1, p. 14) have presented detailed historical reviews of the Reedsville-Martinsburg nomenclatural problems in the central Appalachians, to which the reader is referred.

The fossiliferous beds at the top of the Reedsville and Martinsburg Formations have no formal rock-stratigraphic designation in the literature, although they constitute all or part of a generally recognized upper member of the Reedsville (Horowitz, 1965; Rader and Ryan, 1965; Pierce, 1966; and Butts, 1945). Lithologies in which the fossils occur vary along the outcrop belt, but rock types exhibit an overall north-south trend. Thick to massively bedded sandstones are common in the north and grade into thin- to medium-bedded siltstones, shales and limestones toward the

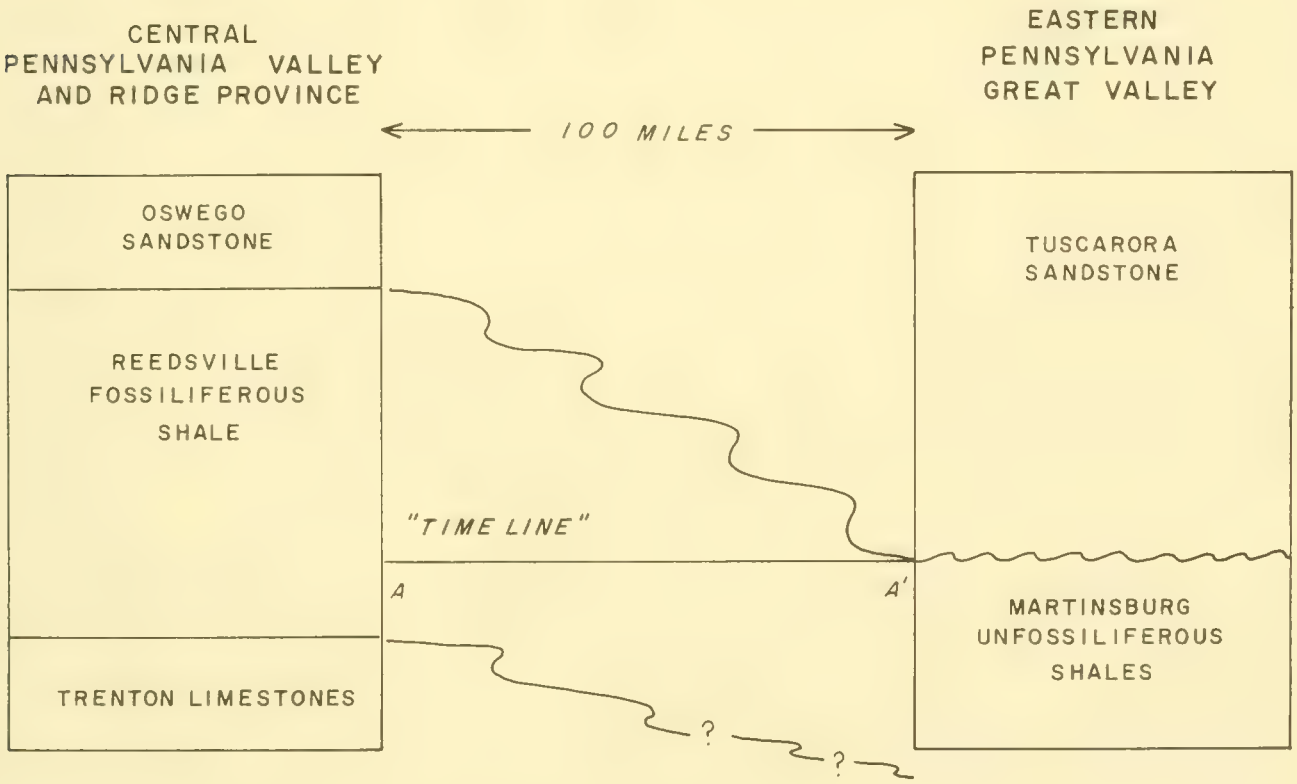


FIG. 4. Correlation of the Upper Ordovician strata in Pennsylvania after McBride (1960). McBride's interpretation emphasizes the concept of lithofacies migration throughout a significant period of geologic time. It should be noted that this interpretation is based on the overall Upper Ordovician stratigraphic and sedimentological setting and has not included the fossil record, although a sparse fauna exists in the Shochary Ridge Sandstone Member of the Martinsburg Formation. Line A-A' connects lithologic units of supposed equivalent age.

south. Figure 5 shows the relative proportions and stratigraphic and geographic distribution of the various lithologies in the central Appalachians. The lower contact of the abundantly fossiliferous strata is commonly gradational into the thinner bedded, finer grained and sparcely fossiliferous rocks, whereas the upper contact, based on bedding, lithology and color characteristics is normally much more abrupt (see Horowitz, 1965, p. 9–22, for definition of the lower contact on slight changes in bedding thickness); the fossiliferous beds of the upper Reedsville and Martinsburg are overlain by Oswego (= Bald Eagle) quartzitic sandstones in central Pennsylvania and eastern West Virginia (Fig. 7), Juniata red shales and sandstones from east-central Pennsylvania to Tennessee, Sequatchie red limestones in Tennessee, and Tuscarora (Massanutten) quartzitic sandstones in eastern Pennsylvania and north-central Virginia (Fig. 2). Some interbedding of the upper fossiliferous Reedsville and the Oswego and Juniata Formations occurs over a few tens of feet, but the upper contact normally appears quite sharp, although it is probably unconformable only in portions of eastern and central Pennsylvania and north-central Virginia (Figs. 2 and 5).

Prior to my study, the *Orthorhynchula* Zone faunas were viewed as a lithologically controlled biofacies (Butts, 1945, p. 5; Woodward, 1951, p. 335 ff.), or possibly a local range zone or teilzone (Butts, 1940, p. 217). This latter interpretation is based on the fact that the characteristic fauna of the *Orthorhynchula* Zone, mainly abundant rhynchonellid and linguloid brachiopods and some bivalve molluscs, have been found at the same stratigraphic position (i.e., near or at the top of the Reedsville or Martinsburg) in thin-bedded limestones, argillaceous limestones and thick-bedded quartz sandstones. This may lend some credence to an interpretation of the *Orthorhynchula* Zone faunas as significant time-stratigraphic markers in the central Appalachian Valley and Ridge Province.

The fauna of the central Appalachian *Orthorhynchula* Zone is typified not only by large numbers of the rhynchonellid *Orthorhynchula linneyi,* but also by abundant linguloid brachiopods, bellerophontid gastropods, and modiomorphid, ambonychiid and nuculoid bivalve molluscs. Other fossiliferous strata at the top of the Reedsville and Martinsburg include abundant species of orthid, strophomenid and atrypid brachiopods, pleurotomariacean gastropods, trepostomatous bryozoans, crinoids and occasionally abundant trilobites (see Fig. 7 which diagrams a composite columnar section typical of eastern West Virginia and south-central Pennsylvania, showing bedding features and lithologies as well as major faunal components).

I have interpreted the *Orthorhynchula* Zone faunas as containing two fossil community zones (see Berry, 1966, p. 1492) — the *Orthorhynchula–Ambonychia* Community in southern Pennsylvania and central Virginia, and the *Zygospira–Hebertella* Community in southwestern Virginia and northern Tennessee. The species in the fossiliferous strata comprising the third community defined in this study, the *Sowerbyella–Onniella* Community, were never considered to be part of the *Orthorhynchula* Zone by earlier workers, since this community contains no large rhynchonellid or linguloid brachiopods. The fossiliferous strata comprising the *Orthorhynchula–Ambonychia* and *Sowerbyella–Onniella* Communities are, however, occasionally interbedded in south-central Pennsylvania and northern Virginia (Fig. 6), although the faunas are rarely mixed. My interpretations, of course, do not negate the time-stratigraphic significance of the zonal faunas, but rather emphasize the environmental limits of each

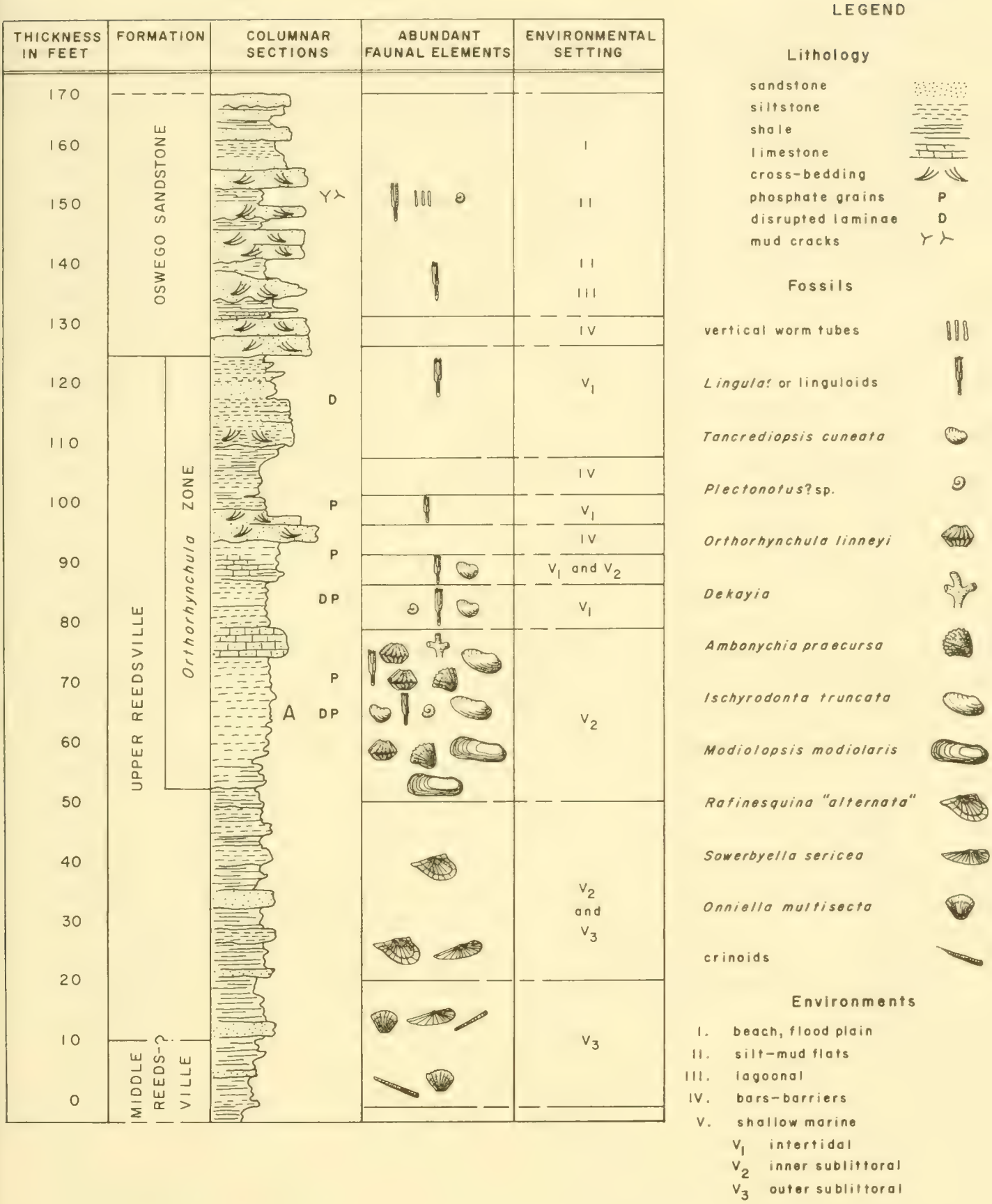


FIG. 7. Composite upper Reedsville—Oswego columnar section from eastern West Virginia and south-central Pennsylvania emphasizing a detailed lithologic and faunal correlation. Only abundant faunas are noted and the interpretation of environmental settings are outlined in text. Top of the *Orthorhynchula* Zone placed at last occurrence of *Lingula*? and bottom of zone where abundant *Modiolopsis modiolaris* disappear. The letter "A" marks a bed in that portion of the section at locality 203 in West Virginia that was sectioned and photographed (see Pl. 1).

fossil community and place it in environmental perspective, both temporally and geographically.

It is generally held that the orthid, strophomenid and spiriferid brachiopods and the modiolopsid bivalves in the upper Reedsville strata in southern Pennsylvania and eastern West Virginia indicate that these strata are time-correlative with those of the Pulaski Sandstone of western New York. (See Woodward, 1951, p. 371–376; Willard, 1943, p. 1103–1106; Butts, 1940, p. 218). The orthid and atrypid brachiopods in these fossiliferous units in southwestern Virginia and northern Tennessee (Butts, 1940, p. 218), as well as the Pulaski brachiopod and bivalve mollusc fauna (Foerste, 1924; Ruedemann, 1925a), have been correlated with those in the Fairview Formation in the Cincinnatian type area; this correlation implies a lower Maysvillian age for the fossiliferous strata at the top of the Reedsville. Peck (1966) and Ford (1965, 1967), in their revision of the Upper Ordovician formations in the Maysville and Cincinnati regions, have retained the term Fairview Formation and have redefined it as a rock-stratigraphic unit, but it is essentially the same unit as the earlier faunally defined "Fairview Formation" because the faunal breaks occur where major lithologic changes take place; therefore, the correlation originally made will remain about the same (John Pojeta, pers. comm.).

The stratigraphic interval represented by the *Orthorhynchula* Zone and other stratigraphically equivalent fossiliferous units at the top of the Reedsville and Martinsburg Formations varies between 50 and 200 feet, reaching a maximum thickness in central and eastern Pennsylvania and south-central Virginia, and thinning to less than 100 feet in eastern Western Virginia and north-central Virginia (Fig. 5). Thickness measurements in southwestern Virginia and northern Tennessee vary between 50 and 150 feet. Specifically, the *Orthorhynchula* Zone constitutes about the upper 20 to 60 feet of the upper Reedsville in south-central Pennsylvania. The zone thickens to about 100 feet in eastern West Virginia, and thicknesses of 50 to 125 feet are common in west-central and south-central Virginia, where the total thickness of the fossiliferous rocks of the upper Reedsville may range from 100 to 200 feet.

Figure 8 outlines the general geographic limits of the fossiliferous upper Reedsville and Martinsburg rocks, which extend from the western edge of the Appalachian Valley and Ridge Province into the Great Valley to the east. The maximum width of the belt occasionally approaches 100 miles, but it is usually less than 50 miles wide. (Note that Fig. 8 has a palinspastic base.) The length of the outcrop belt is over 600 miles.

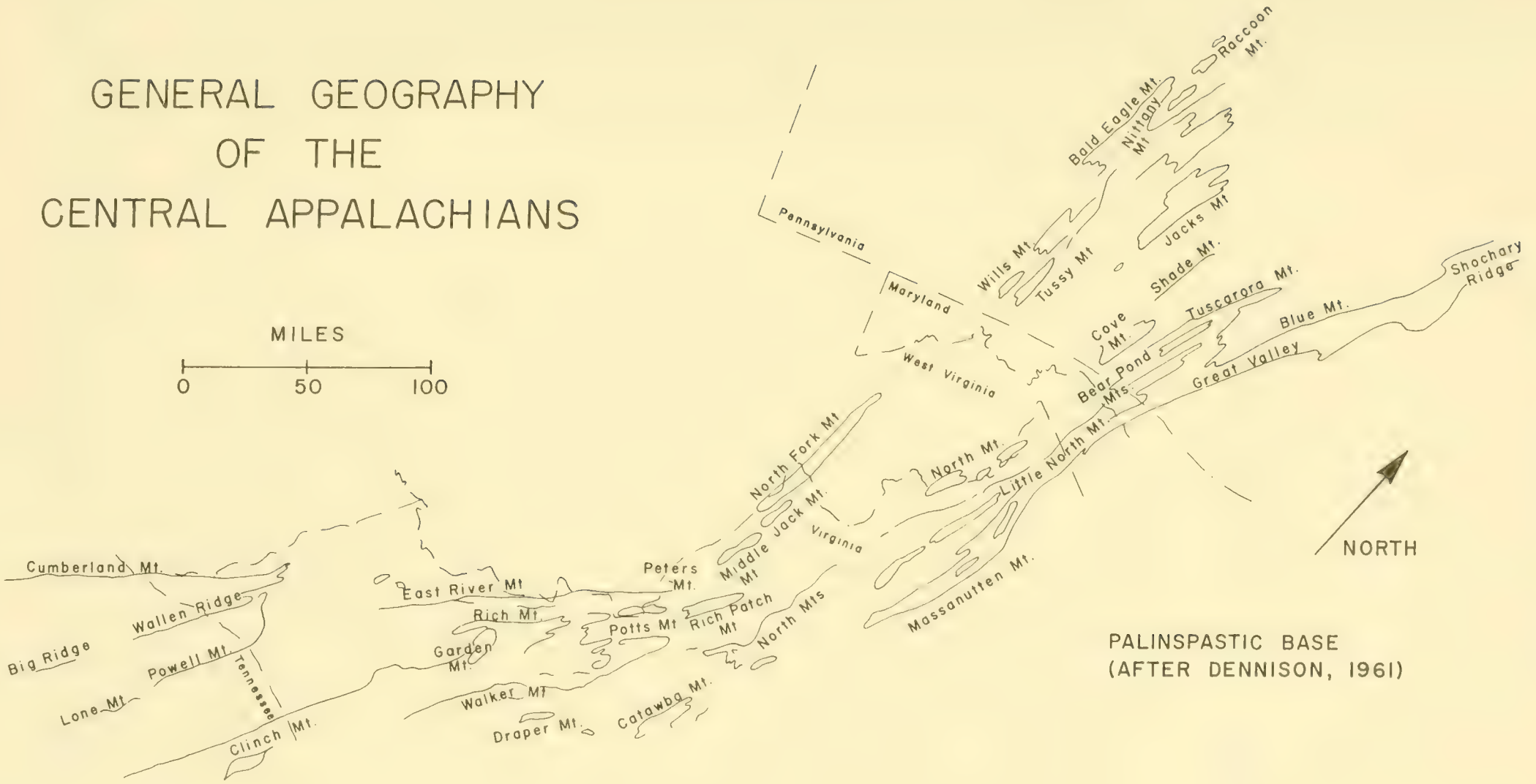


FIG. 8. Outline of geographic limits of the fossiliferous upper Reedsville and Martinsburg rocks, which extend from the western edge of the Appalachian Valley and Ridge Province into the Great Valley to the east. The lines on the map are the Reedsville-Martinsburg outcrop pattern and hence outline the Appalachian ridges where the rocks are exposed.

ENVIRONMENTAL INTERPRETATIONS FROM STRATIGRAPHIC AND SEDIMENTOLOGICAL EVIDENCE

Earlier sedimentological and stratigraphic studies in the north-central Appalachian Upper Ordovician have provided a broad outline of the probable environments of deposition of these predominantly clastic sediments. Most investigators working in the Oswego (= Bald Eagle) and Juniata Formations that overlie the fossiliferous units at the top of the Reedsville and Martinsburg(?) Formations agree that the source of the sediment was to the east; these workers have also provided evidence of a progressive uplift of the source area, resulting in a westward progradation of the depositional environments throughout Late Ordovician time. Evidence of this regression comes from numerous previously measured sections that show a gradual increase in grain size from the shales of the lower part of the Reedsville upward through the sandstones and conglomerates of the Oswego and Juniata. The geometric shape and primary sedimentary structures of the upper parts of the Oswego and the entire Juniata support the hypothesis of an eastern source area and westward progradation, as both exhibit predominantly west-dipping cross beds that outline a broad, fan-shaped regional current pattern. Figure 9 is a reconstruction of the east to west progradation of the Upper Ordovician formations based on the stratigraphic-sedimentological evidence. The "time lines" are diagrammatic, not based on specific faunal evidence, but again reflect the overall stratigraphic pattern. The apron-like thinning of the Oswego and the associated decrease in the overall grain size from east to west imply a source area extending from eastern Pennsylvania to northern Virginia, and a westward transport of detritus (Yeakel, 1962, p. 1533). Measurements of cross-bedding in the Juniata sandstones reveal a dispersal pattern similar to that of the Oswego. Therefore all available evidence points to a general north-south strike and westward primary dip of the Late Ordovician sea floor.

Previous investigators working in the north-central Appalachians have interpreted the siltstones and shales of the lower and middle parts of the Reedsville Formation as marine and the sandstones of the upper parts of the Oswego and the Juniata Formations as alluvial or flood plain deposits. There is much less agreement as to the depositional environments of the sandstones and siltstones of the upper Reedsville and of the sandstone of the lower Oswego in southern Pennsylvania, eastern West Virginia and west-central Virginia. A Late Ordovician littoral environment exists in these rocks between the obviously marine and obviously terrestrial beds.

Grabau (1913, p. 440–441) proposed that the Oswego sandstones in Pennsylvania represented the terrestrial part of a prograding delta and that the Reedsville formed its marine equivalent. Yeakel (1962, p. 1534) generally agreed with Grabau and at-

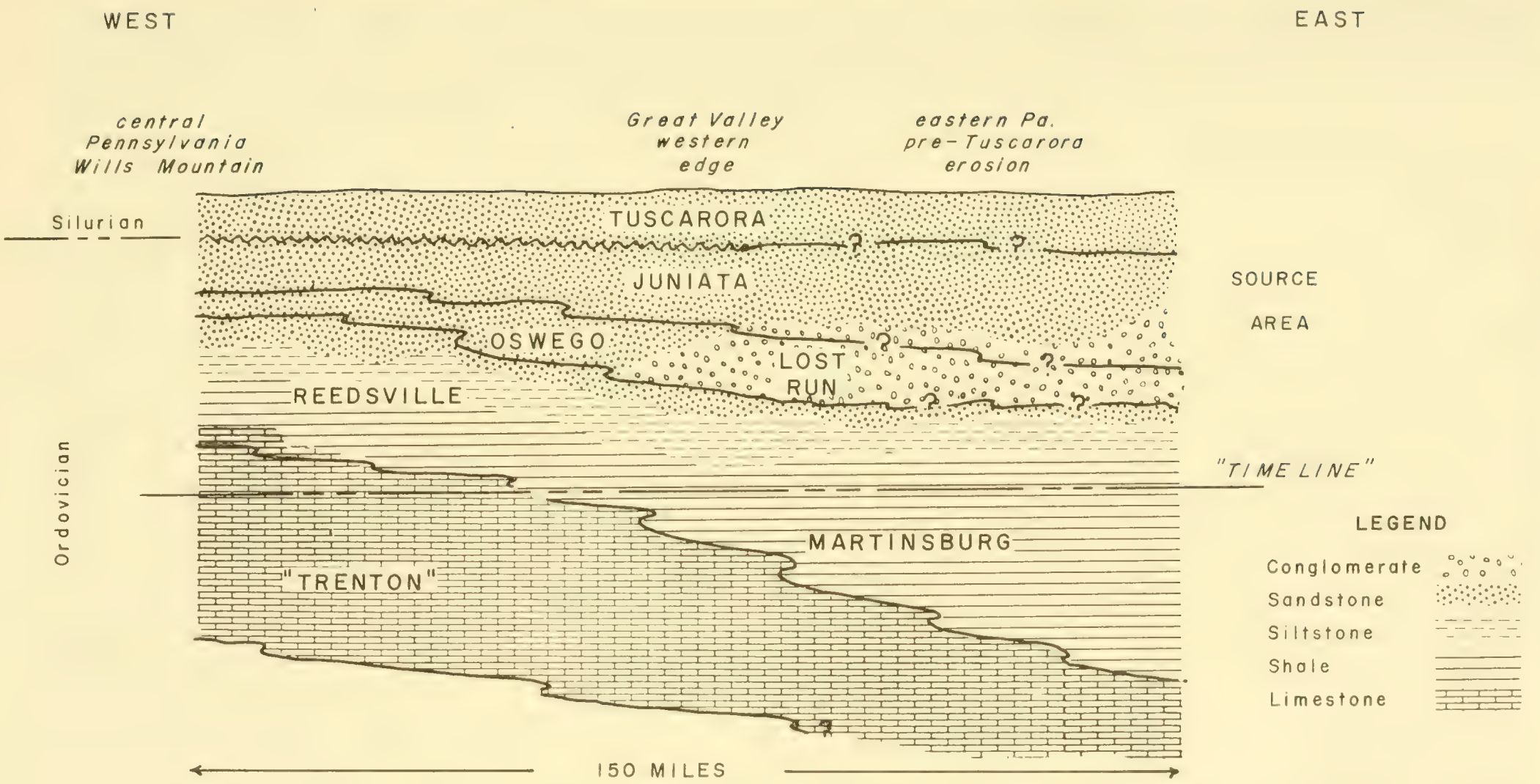


FIG. 9. Reconstruction of a probable east to west migration of the Upper Ordovician formations in Pennsylvania and northern Virginia. Interpretations are made from previous stratigraphic and sedimentological studies (McBride, 1960; Yeakel, 1962; Horowitz, 1965). The source of terrigenous clastics was to the east and uplift appears to have occurred throughout the Late Ordovician. This figure is diagrammatic and there is no inference as to rates of progradation. The interval represented by the *Orthorhynchula* Zone would lie at the top of the Reedsville Formation in central Pennsylvania.

tempted to demonstrate that the Bald Eagle (= Oswego) was largely an alluvial deposit. Pierce (1966, p. 29), however, working in the same area, interpreted the Oswego as a shallow marine deposit. Krynine (1960) considered the transitional Oswego-Reedsville complex in south-central Pennsylvania as a beach, lagoonal and open-sea system. Woodward (1951, p. 381), in his review of the Ordovician stratigraphy of eastern West Virginia, interpreted the lower part of the Oswego as a shallow marine deposit and the upper part as a subaerial delta.

Two recent studies compared the Late Ordovician environments with more precisely defined modern depositional regimes. Horowitz (1965, 1966), working in south-central Pennsylvania and eastern West Virginia, revised Grabau's (1913) concept, and pictured a broad, nearshore marine, deltaic environment; Horowitz found analogues in the uppermost Reedsville and lower Oswego for Recent topset, foreset and bottomset beds. Thompson (1967), also working in south-central Pennsylvania, followed Krynine (1960) in proposing a beach, lagoonal and barrier-bar model for the same sequence of upper Reedsville and lower Oswego sediments. Horowitz (1965, 1966) considered the fossiliferous shales, shaly siltstones and sandstones at the top of the Reedsville to be the foresets of a Late Ordovician delta or coalescing smaller deltas, whereas Thompson (1967) believed them to represent a very shallow marine, almost intertidal environment situated immediately seaward of a barrier-lagoonal complex.

Irrespective of the details of the Late Ordovician depositional environment, the sediments of the upper Reedsville Formation formed nearshore marine deposits, possibly intertidal in part, but certainly inner sublittoral. In Pennsylvania and West Virginia these sandstones and siltstones are moderately sorted, perhaps suggesting deposition in areas which were occasionally washed by waves and currents. Cross-laminae are evident and presumably were produced by gentle current reworking, but more often in the upper parts of the fossiliferous horizon (especially in Pennsylvania and West Virginia) the effect of washing appears to have been destroyed by the activity of burrowing organisms or soft-sediment deformation. Plate 1 is a section cut from the *Orthorhynchula* Zone in eastern West Virginia (locality 203, A-6304, about 70 feet below the Oswego-Reedsville contact, see Fig. 8). Donald Rhoads (pers. comm.) has pointed out similar disrupted sedimentary structures in a core taken from a Recent muddy silt environment in Buzzards Bay, Massachusetts, in about 20 meters of water (Station R of Sanders, 1958, p. 246, fig. 1). The mixing of the Recent sediment is attributed to reworking by organisms.

One other indication of the possible shallow water origin for the upper Reedsville sediments is found in the occurrence of fine to medium sand size phosphate grains that often occur in the massive, biogenically reworked layers (see Pl. 1). Unfortunately the origin of shallow water phosphate is not well known. Bushinski (1964) and d'Angeljan-Chatillon (1965, 1967) have surveyed the subject, contrasting the scanty Recent observations with better documented geologic examples, most of which seem in some need of reinterpretation. D'Angeljan-Chatillon (1965), studying the marine platform off the west coast of Baja California, has found that the highest concentration of phosphate grains occurs in a sandy shelf sediment from the coastal lagoons to 100 meters water depth. The grains are well sorted, possibly because of their mode of formation as internal molds of Foraminifera, and encrust detrital materials. The replacement of internal molds and fecal pellets by phosphate appears to require the

following conditions: 1) slightly positive Eh; 2) shallow depth; 3) high organic productivity (upwelling waters from deep ocean basins rich in P_2O_5 will encourage high secondary productivity in shallow water, see Fig. 11); and 4) low rate of sedimentation (concentrations found only in condensed deposit).

Bushinski (1964) hypothesized from the data of Bruevitch and Saitzeva (1958), working in the Bering Sea, that muddy silts situated in hollows between shoals are especially rich in dissolved phosphate. The incipient grains would form in the oxygen-poor hollows (Youssef, 1965), and intermittent periods of turbulence reaching into this stagnant regime would rework and redistribute the partially consolidated grains on the shallow marine shelf. The biochemical and bacterial processes of phosphate concentration in shallow water areas are, however, virtually unknown.

The phosphate in the central Appalachian Upper Ordovician deposits appears to encrust finer detrital quartz sands and silts, in addition to being complete or partial internal molds of small bellerophontid gastropods (*Plectonotus*? sp.); associated with these grains are phosphatic shell debris (usually linguloid brachiopod fragments), phosphate cement and small apatite crystals. The original calcareous shell material is usually dissolved or worn away, but occasionally the walls of trepostomatous bryozoans (*Dekayia*) show complete replacement of the calcite by phosphate. The grains usually constitute less than 5 per cent of the sediment, are usually smooth and appear to have undergone some agitation, but seem to have formed in areas generally protected from strong wave and tidal current activity. The currents were strong enough to wash out much of the clay-sized fraction and alter the shape of most of the grains (e.g. irregularly shaped internal molds of *Plectonotus*? sp. seem to have resulted from reworking). Phosphate-encrusted sand grains are usually well sorted, but the phosphate grains are rare where there is a high percentage of sands and normally are found within the highly reworked beds interbedded with the cross-bedded bar and barrier sands. This association probably indicates a shallowing trend accompanied by a decrease in oceanic circulation. The occasional phosphate pseudomorphs of calcareous shell material (e.g., *Dekayia*) and the complete biogenic reworking of the muddy silts presumably indicate a slow accumulation of sediments. The P_2O_5 is probably taken out of the nearshore waters by abundant planktonic organisms that upon death sink to the shallow bottom; in order for the phosphate to remain, there must be little circulation on the way down and no resuspension of the bottom mud until the grains have had a chance to harden and to replace shell material.

In a summation of the previous sedimentological-stratigraphic interpretations of the central Appalachian Upper Ordovician strata, it is apparent that the transitional nearshore marine environments in the upper Reedsville and lower Oswego Formations appear to have covered an area from south-central Pennsylvania into eastern Virginia and adjoining parts of west-central Virginia. The Oswego Sandstone in north-central Pennsylvania is, however, alluvial or flood plain in origin (Yeakel, 1962), with occasional large-scale festoon cross beds. The Oswego-Reedsville contact in this area of the central Appalachians is probably erosional. Here a major deltaic complex may have developed, accompanied by high rates of sedimentation and vigorous erosion as the complex prograded westward. The erosional unconformity becomes more evident to the east with an associated development of a thick conglomeratic facies. It seems reasonable that near this major terrigenous source area a high sediment influx prevented either the formation or the preservation of many of the

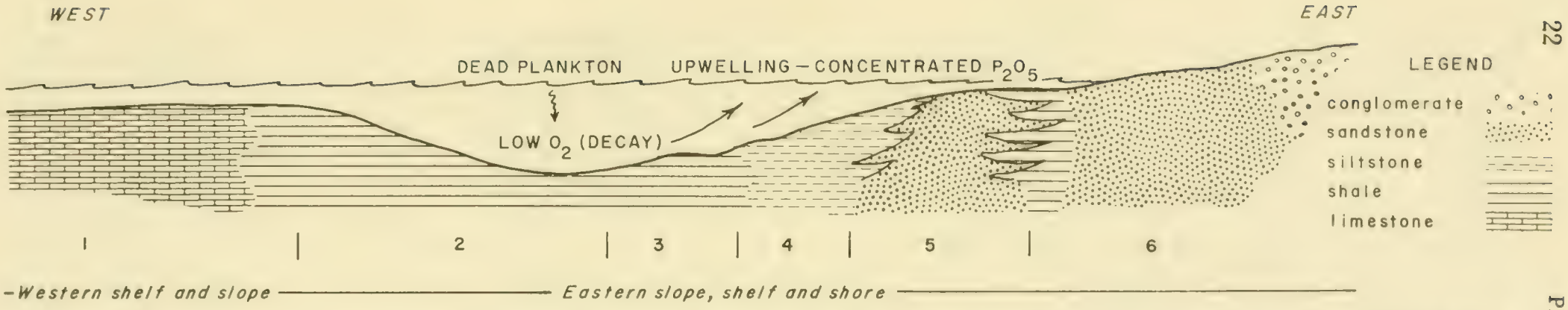


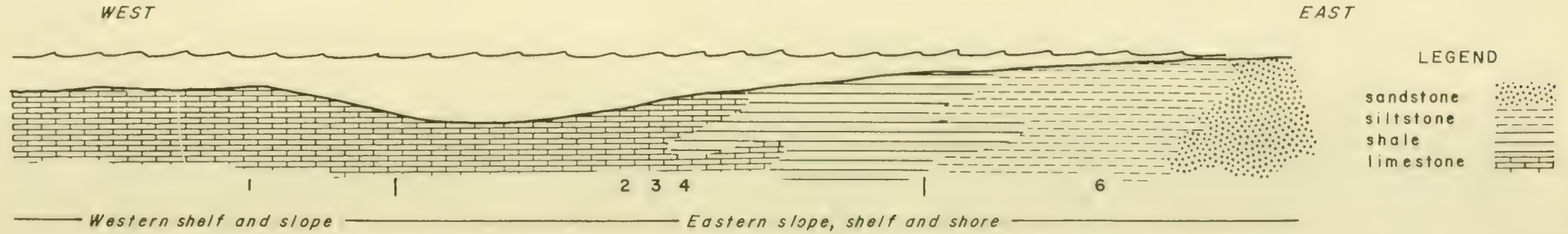
FIG. 10. Reconstruction of the onshore to offshore profile (east-west) during the Late Ordovician in the north-central Appalachians. Numerals refer to bathymetric environments and are also used in Figures 11 and 12.

Western Shelf and Slope(?)

1. Cincinnatian limestones and shales—shallow sublittoral, continental seas.
2. Lower Reedsville mud—bathyl(?) and outer sublittoral area of low O_2 concentration, stagnant basin environment; therefore, decay and upwelling of P_2O_5 eastward toward shallow shelf providing for high primary productivity.

Eastern Slope(?), Shelf and Shore

3. Middle Reedsville mud, silt and limestone coquinas—outer sublittoral and bathyl(?), turbidites of eastern origin common.
4. Upper Reedsville muddy silts and sands—inner sublittoral and possibly intertidal, prolific bottom fauna, *Orthorhynchula* Zone, results from upwelling from depths thus allowing high primary productivity.
5. Lower part of Oswego Sandstone, coarse cross-bedded sands and interbedded muds—beach, bar and lagoonal environments.
6. Upper part of Oswego Sandstone, Lost Run Conglomerate and Juniata Sandstone—deltaic, flood plain and alluvial environments.



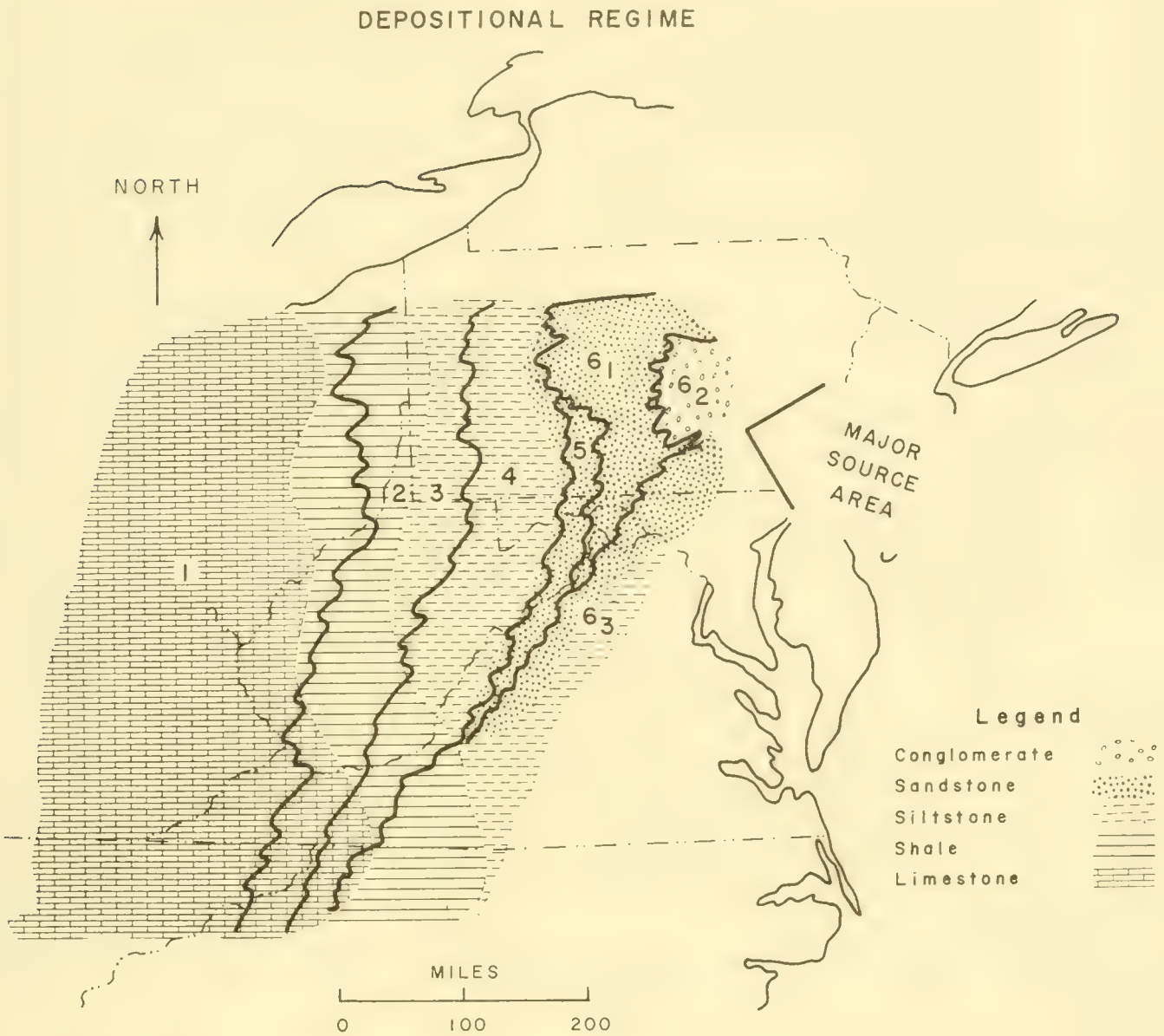


FIG. 12. Reconstruction of the depositional environments during the Late Ordovician in the central Appalachians (see Figs. 10 and 11 for a more complete description of the environments).

1. Western shelf carbonates—Cincinnatian limestones.
2. and 3. Western slope (?) and eastern slope (?), outer shelf muds and silts—lower part of Reedsville.
4. Eastern inner shelf silts and sands—upper part of Reedsville.
5. Barrier and beach coarse sands, lagoonal muds—lower part of Oswego Sandstone.
6. Flood plain silts and sands, alluvial sands and conglomerates.
   6_1—Oswego 6_2—Lost Run 6_3—Juniata

FIG. 11. Reconstruction of the onshore to offshore profile (east-west) during the Late Ordovician in southwestern Virginia and northern Tennessee. Numerals refer to bathymetric environments and are also used in Figures 10 and 12. Note that there are no lower Oswego beach, bar and lagoonal environments (5. in Fig. 10) in the south.

Western Shelf: 1. Cincinnatian limestones—shallow sublittoral, continental seas.
Eastern Shelf and Shore: 2. 3. and 4. Reedsville silty muds, muds and lime muds—sublittoral and possibly intertidal environments. 6. Juniata muds, silts and sands—flood plain and alluvial environments.

ephemeral shoreline features — barrier, bar and lagoonal deposits — that are seen farther to the south in south-central Pennsylvania, eastern West Virginia and north-central Virginia. It does seem possible, however, that some of the considerable quantities of the lower Oswego barrier-bar-forming sands may have initially been deposited in central Pennsylvania and then redeposited by longshore currents to the south.

The Oswego (= Bald Eagle) is not present south of west-central Virginia and I believe that near Middle Mountain, Virginia (Fig. 1, loc. 194) the few tens of feet of Oswego Sandstone represent the termination of the north-to-south longshore deposits. The reddish Juniata sandstones are more poorly sorted in the south-central Appalachians and contain a notably higher percentage of shale beds. The entire depositional regime in southwestern Virginia and northern Tennessee appears to represent a low-energy environment, probably a broad fluctuating subaqueous and subaerial flood plain, receiving much less terrigenous clastic material than the more northern areas.

Figures 10 to 12 combine these concepts into cross-sections together with a map of the Upper Ordovician sedimentological environments as they probably appeared on the Late Ordovician shelf in the central Appalachians. This reconstruction will provide the framework on which the zoogeographic distributions of the Late Ordovician faunal communities will be charted.

FAUNAS

INTRODUCTION

Numerically dominant taxonomic groups throughout the central Appalachian Upper Ordovician fauna are the bryozoans, the brachiopods, the gastropods and the bivalves. Trilobites and crinoids are abundant but only in the north-central Appalachians and presumably are restricted ecologically. The fossils are distributed throughout the upper Reedsville and equivalent Martinsburg strata; they are uncommon in the lower parts of the Oswego in the north-central Appalachians and in the lower parts of the Juniata and Sequachie in the south. The fossils, concentrated in layers and lenses, are usually preserved as composite, internal or external molds. The valves of bivalves and brachiopods are frequently disarticulated but show little evidence of surface wear or breakage. Obvious pelomorphic distortion of the fossil material has resulted from compaction on the bedding plane and from subsequent tectonic events in the folded and faulted Valley and Ridge Province. Calcareous shell material is never present in the gastropods, is scarce and completely recrystallized in a few bivalves, and has been preserved only in the brachiopods and bryozoans.

Table 1 is a list of the genera and/or species which are discussed in the chapter on systematic paleontology. About 5,100 specimens were collected from 164 localities

TABLE 1. Genera and/or species reviewed in the chapter on systematic paleontology.

BRYOZOA
- *Monticulipora*
- *Dekayia*
- *Batostomella*
- *Amplexopora*
- *Hallopora*

BRACHIOPODA
- *Lingula?*
- *Hebertella sinuata*
- *Onniella multisecta*
- *Sowerbyella (Sowerbyella) sericea*
- *Rafinesquina "alternata"*
- *Orthorhynchula linneyi*
- *Zygospira modesta*
- *Zygospira recurvirostra*

GASTROPODA
- *Plectonotus?* sp.
- *Bucania* sp.
- *Loxoplocus (Lophospira) abbreviata*
- *L. (L.) perangulata*
- *L. (L.) ventricosta*
- *Ruedemannia? lirata*
- *Sinuopea?*
- *Murchisonia?*

BIVALVIA
- *Tancrediopsis cuneata*
- *Ctenodonta? pulchella*
- *Praenucula levata*
- *Ambonychia radiata*
- *A. praecursa*
- *A. cultrata*
- *?A. byrnesi*
- *Pterinea (Caritodens) demissa*
- *Modiolopsis modiolaris*
- *Ischyrodonta? truncata*
- *Lyrodesma poststriatum*

throughout the central Appalachians. There are about 35 abundant species in the rocks of the central Appalachian Upper Ordovician; some less numerous species are not described but occasionally are referred to in various systematic discussion. No attempt has been made to compile a complete list of central Appalachian Upper Ordovician species; the reader is referred to Butts (1941) and Woodward (1951) for such lists.

No specific sampling techiniques for determination of species density had been designed prior to the start of the project; initial field examinations of a few well-known exposures emphasized the difficulties of utilizing a standardized sampling technique (e. g. counts of specimens per unit area of rock) because of the wide variation in area of exposed rock from locality to locality. Several random grid and line methods were attempted at a few exposures and at various stratigraphic intervals in order to determine the absolute abundance or density of particular species (see Ager, 1963, p. 220–230), but it was decided that in this introductory study reasonably accurate estimates of species density could be obtained if a relative scale of taxonomic density was constructed and applied at each locality. Table 2 shows this relative scale and the equivalent absolute scale. Species ranking at 3 or greater on the relative scale (i.e., specimens numbering 25 or more per 100 square feet) are considered to be abundant. Table 3 (in pocket) is a compilation of the relative species abundances at each locality sampled in the central Appalachians and forms the basis for the synthesis of species into multi-species populations and communities.

TABLE 2. Taxonomic density scale.

Relative abundance notation	Absolute number of specimens per 100 square feet
1	1–9
2	10–24
3	25–99
4	100–250
5	250

Taxa were identified in the field and relative abundance recorded at each locality, along with the stratigraphic relationships and associated lithology. At only 37 of the 164 localities were the actual absolute counts of species density recorded. These preliminary results were refined in the laboratory after the taxa had been re-examined. I found that the density of the most abundant species often varied from 3 to 5 on the relative abundance scale only a few tens of miles apart. This variation may reflect actual differences in density, but in some cases may be an artifact of the areal extent and degree of weathering of the exposure. What is important, however, is the consistent stratigraphic and zoogeographic re-occurrence of these same species, which permits the outlining of Ordovician faunal populations and communities.

ZOOGEOGRAPHY

The distributional patterns of the central Appalachian Upper Ordovician bryozoans, brachiopods, gastropods and bivalves are shown in Figures 13, 14, 16 and 17. By

systematically segregating each of these major faunas it was hoped that the distributional patterns, both geographically and stratigraphically within the upper Reedsville, would be distinctive enough to aid in more detailed interpretations of the Late Ordovician marine environments. All inferences and interpretations from this zoogeographic data have been incorporated into the following chapters on paleoautecology and community structure.

Recognition of a systematically consistent portion of a major taxonomic group occupying and dominating a particular geographic region has led to the use of the term "faunal province". Any abrupt change in the faunal composition of the upper Reedsville strata will define a provincial boundary. Provincial overlap takes place and may be accompanied by an intermingling of species or a distinct stratigraphic separation of the faunas, still within the upper Reedsville strata.

Bryozoa

The distribution of the bryozoans of the central Appalachian Upper Ordovician is shown in Figure 13. The bryozoan fauna can be divided into three smaller faunal provinces designated I, II and III. These faunal provinces are strictly defined by the existing geographic limits of the bryozoan faunas and incorporate no interpretations of probable Ordovician distributional patterns which are reserved for the following two chapters. Two of the provinces show domination by a single genus (Table 4). Generally the provinces are distinct geographically, although there is some faunal overlap between bryozoan provinces II and III in south-central Virginia (Fig. 13). This overlap between II and III shows no stratigraphic separation but rather a mingling of the faunas. Bryozoan province I, although exhibiting considerable geographic separation from province II, is believed to occur considerably lower in the upper Reedsville stratigraphic section than do those faunas of province II. All of the abundant bryozoan genera composing these three faunal provinces are trepostomes.

TABLE 4. Bryozoan faunal provinces. See also Fig. 13.

	Location	Abundant Fauna
I	North-central Pennsylvania	*Hallopora*
II	Eastern West Virginia and west-central Virginia	*Dekayia*
III	Southwestern Virginia and northern Tennessee	*Monticulipora* *Dekayia* *Batostomella* *Amplexopora* *Hallopora* *Heterotrypa* Peronoporid

Brachiopoda

The zoogeographic pattern of the brachiopods also outlines three main faunal provinces, designated I, II and III (Fig. 14). There is a more pronounced geographic overlap of the brachiopod faunas at the boundaries of the provinces, in contrast to the almost complete separation of the bryozoan faunal provinces. Table 5 presents the abundant faunal elements in each brachiopod province.

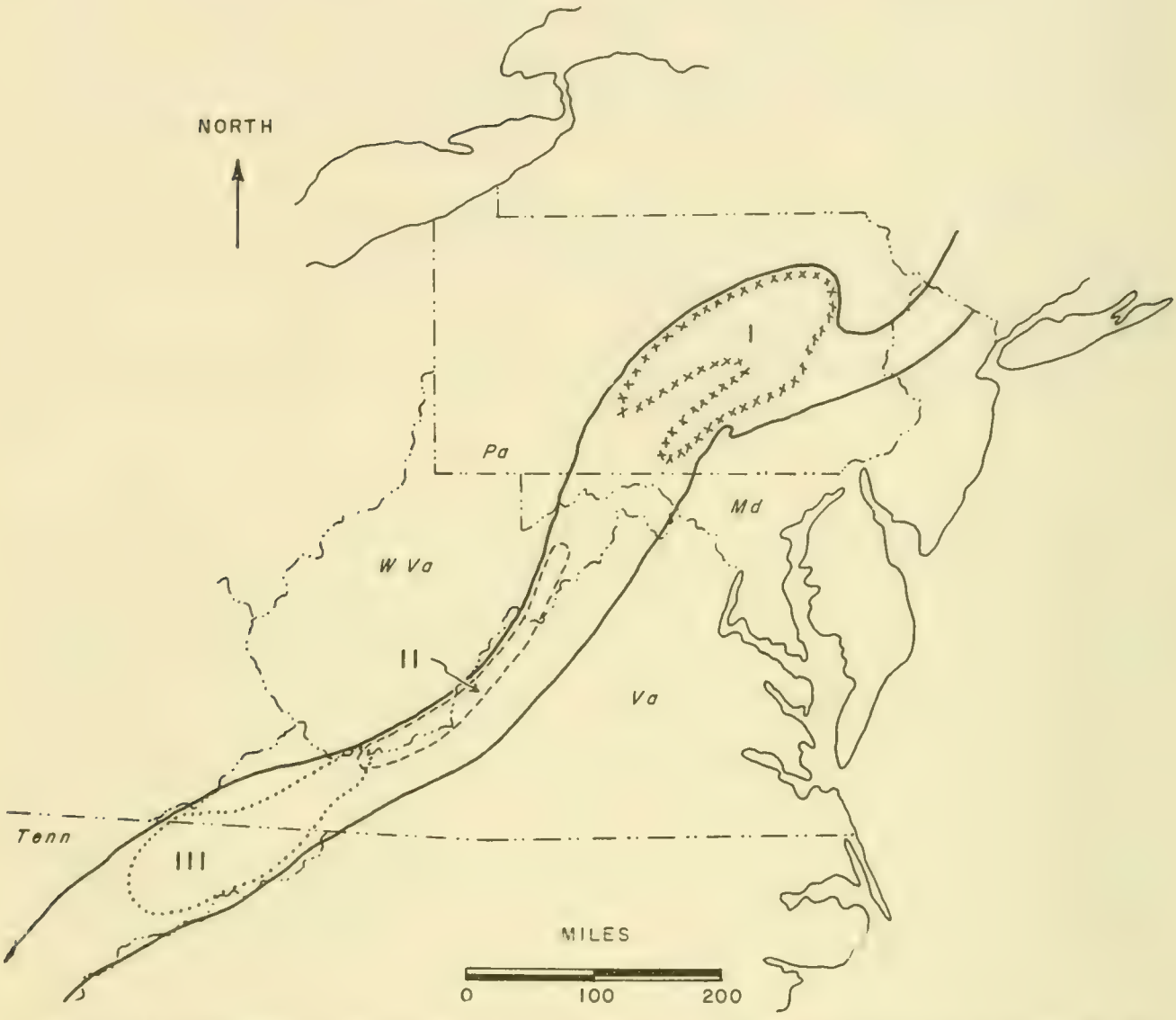


FIG. 13. A generalized outline of the most abundant trepostomatous bryozoan genera in the central Appalachian Upper Ordovician. Three main bryozoan faunal provinces:

I. *Hallopora*
II. *Dekayia*
III. *Monticulipora*
Dekayia
Hallopora
Batostomella
Amplexopora

TABLE 5. Brachiopod faunal provinces. See also Fig. 14.

	Location	Abundant Fauna
I	Eastern Pennsylvania, central Pennsylvania and northern Virginia	*Rafinesquina "alternata"* *Sowerbyella (Sowerbyella) sericea* *Onniella multisecta* *Zygospira modesta*
II	South-central Pennsylvania to south-central Virginia	*Lingula?* *Orthorhynchula linneyi*
III	Southwestern Virginia and northern Tennessee	*Hebertella sinuata* *Zygospira recurvirostra*

BRACHIOPOD ZOOGEOGRAPHY

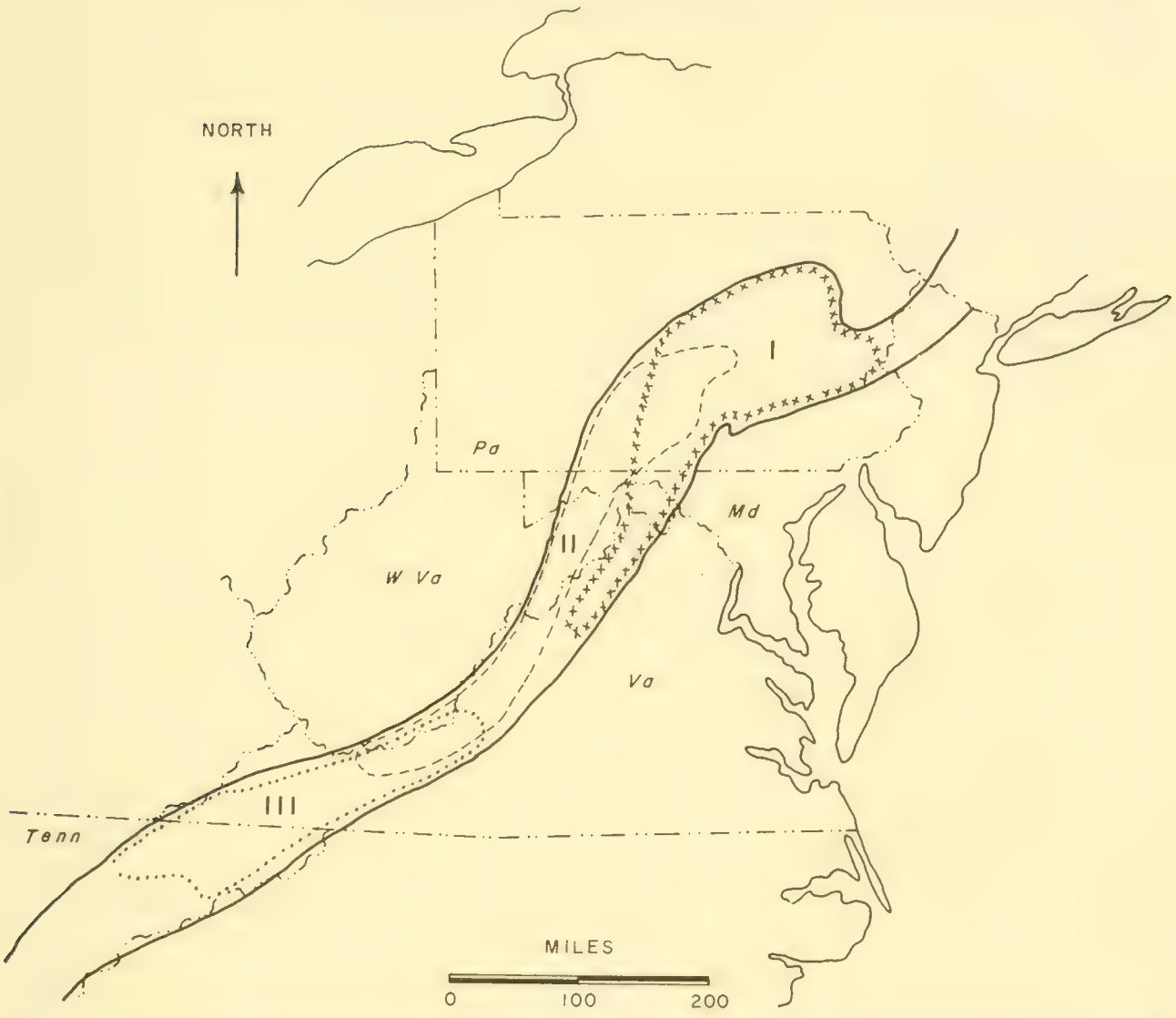


FIG. 14. A generalized outline of the distribution of the most abundant brachiopod species in the central Appalachian Upper Ordovician. The three major brachiopod faunal provinces are:

I. *Sowerbyella* (*Sowerbyella*) *sericea*
   Rafinesquina "alternata"
   Onniella multisecta
II. *Lingula*?
   Orthorhynchula linneyi
III. *Hebertella sinuata*
   Zygospira recurvirostra

Note that overlap of the brachiopod provinces may not result in actual mixing of two faunas since the faunas are separated stratigraphically (see Fig. 15).

Brachiopod province I, predominantly composed of orthids and strophomenids, overlaps brachiopod province II. There is, however, only a very limited mixing of the associated abundant species, because province I is stratigraphically lower than province II (Fig. 15). The fauna of brachiopod provinces I and II exhibit a fairly regular succession of species; in province I strophomenids far outnumber the stratigraphically lower orthids and spiriferids (Fig. 15). Province II, an assemblage of rhynchonellid and linguloid brachiopods, occupies the mid-portion of the central Appalachians and is usually confined to the westernmost upper Reedsville exposures. In province II the

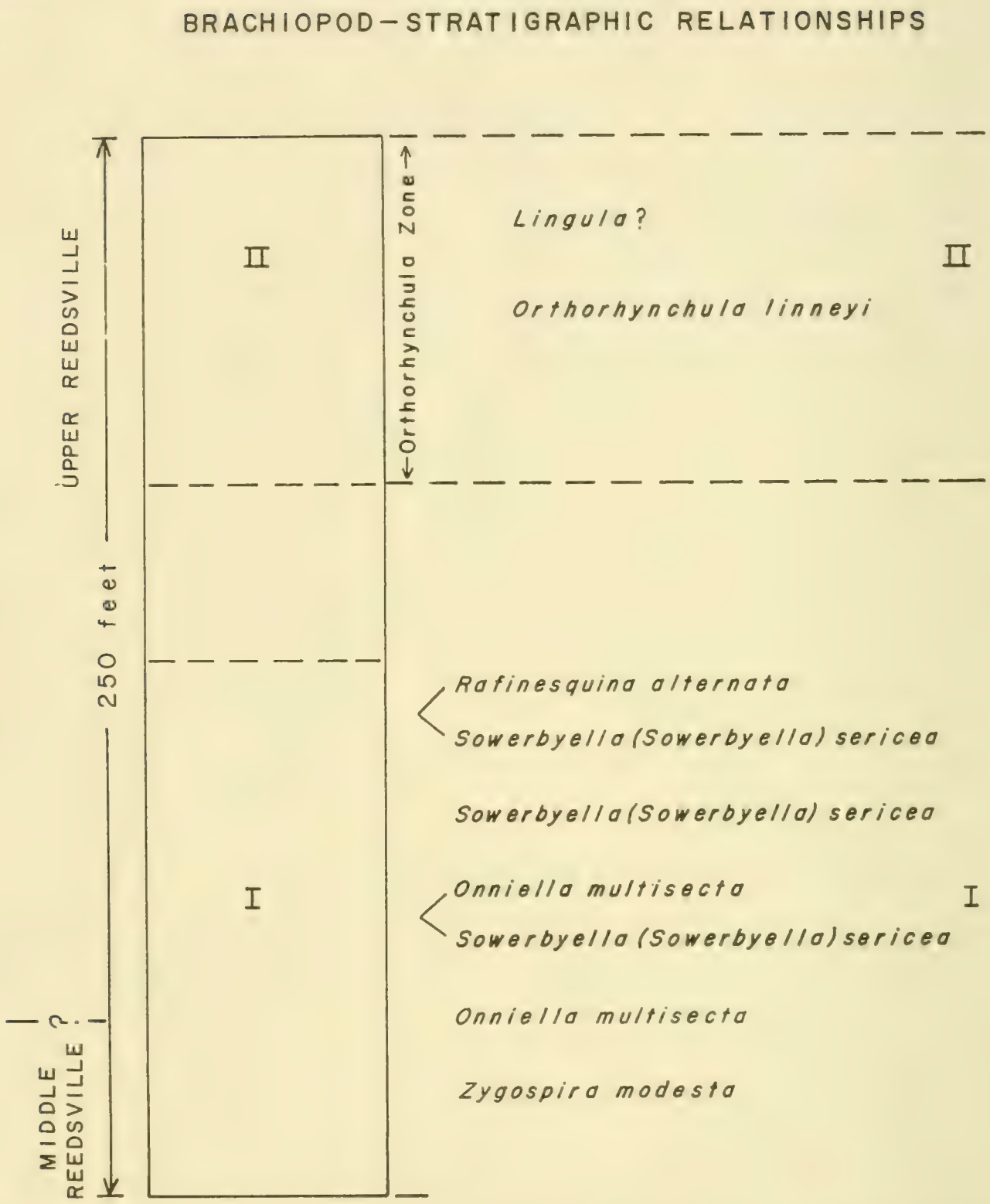


FIG. 15. A composite columnar section from the upper and middle(?) Reedsville in south-central Pennsylvania showing the stratigraphic-faunal separation of brachiopod provinces I and II. See Figure 14 for geographic extent of this overlap.

stratigraphic succession of the faunas follows a pattern whereby the linguloids overlie the rhynchonellids (Fig. 15). Brachiopod province III, dominated by orthids and spiriferids, broadly overlaps province II in southwestern Virginia, but there is no marked stratigraphic separation of the faunas. In the southern part of the mixed zone the linguloids of province II disappear suddenly, but *Orthorhynchula linneyi* is gradually outnumbered by *Hebertella sinuata*. The two dominant species of brachiopod

province III, *Hebertella sinuata* and *Zygospira recurvirostra*, only occasionally occur together; they do not occur in any characteristic stratigraphic order as did the species in brachiopod provinces I and II.

Gastropoda

The distributional pattern of the gastropods is presented in Figure 16. Each of the three gastropod faunal provinces is dominated by species of only one superfamily

FIG. 16. A generalized outline of the distribution of the most common gastropod species in the central Appalachian Upper Ordovician. The three major gastropod faunal provinces are:

I. Pleurotomariid
Loxoplocus (*Lophospira*) spp.
Ruedemannia? *lirata*
Sinuopea?

II. Bellerophontid
Plectonotus? sp.
Bucania sp.

III. Murchisoniid
Murchisonia?

Note that in this instance mixing of the faunas in gastropod provinces I and II occurs where overlap takes place.

(Table 6). Gastropod zoogeography shows strikingly consistent pattern in the central Appalachians throughout the Late Ordovician. Three gastropod provinces have been

TABLE 6. Gastropod faunal provinces. See also Fig. 16.

	Location	Abundant Fauna
I	Central Pennsylvania to central Virginia	Pleurotomariacea *Loxoplocus* (*Lophospira*) *abbreviata* *L.* (*L.*) *perangulata* *Ruedemannia*? *lirata* *Sinuopea*?
II	South-central Pennsylvania to eastern West Virginia	Bellerophontacea *Plectonotus*? sp. *Bucania* sp.
III	Northern Tennessee	Murchisoniacea *Murchisonia*?

delimited and are again designated I, II, and III. The pleurotomariacean gastropods, whose presence delineates gastropod province I, clearly dominate the easternmost exposures of the upper Reedsville and Martinsburg Formations from central Pennsylvania to central Virginia, but are also considerably mixed with the bellerophontacean gastropods of province II in southern Pennsylvania and south-central Virginia. Where this overlap of province I and II faunas takes place there is no noticeable stratigraphic separation of the faunas, but the stratigraphic range of the faunas of province I, the pleurotomariaceans, is much greater than that of the bellerophontaceans of province II which appear to be more confined to the uppermost portions of the upper Reedsville. The bellerophontaceans are also normally limited to the westernmost exposures of the upper Reedsville Formation along this same part of the strike belt. The murchisoniacean gastropods, which constitute gastropod province III, are geographically distinct and not mixed with the dominant northern faunas but appear to occur at the same stratigraphic horizon as the bellerophontaceans of province II, hence occupying the uppermost portions of the upper Reedsville.

Bivalvia

The north-south zoogeographic pattern outlined by the Upper Ordovician Bivalvia in the central Appalachians is quite similar to that of the Brachiopoda (Fig. 17, cf. Fig. 14). The bivalve faunas are, however, often restricted to the westernmost exposures of the upper Reedsville Formation. As in other instances, three bivalve provinces have been delimited, and each of these is characteristically dominated by two or three abundant species (Table 7).

Bivalve province I occupies much of central Pennsylvania, with only locally abundant nuculoid and actinodontoid bivalve molluscs. The overlap with province II, a diverse assemblage of mussel-like bivalves, in south-central Pennsylvania shows a marked stratigraphic separation of the two faunas (Fig. 18). The species of bivalve province I are found from 100 to 150 feet lower in the section than those of province II. The fauna of bivalve province II shows the greatest number and diversity of the Bivalvia in the central Appalachians. The four dominant bivalve species in province

II are not randomly mixed; rather, they occur in a characteristic stratigraphic order with *Tancrediopsis* and *Ischyrodonta* overlying *Ambonychia* and *Modiolopsis* (Fig. 18). In addition *Modiolopsis modiolaris* dominates bivalve province II in the more easterly exposures in central Virginia; *Tancrediopsis cuneata* and *Ambonychia praecursa* are dominant in south-central Pennsylvania and eastern West Virginia. *Tancrediopsis cuneata* and *Ischyrodonta truncata* are only occasionally found on the same

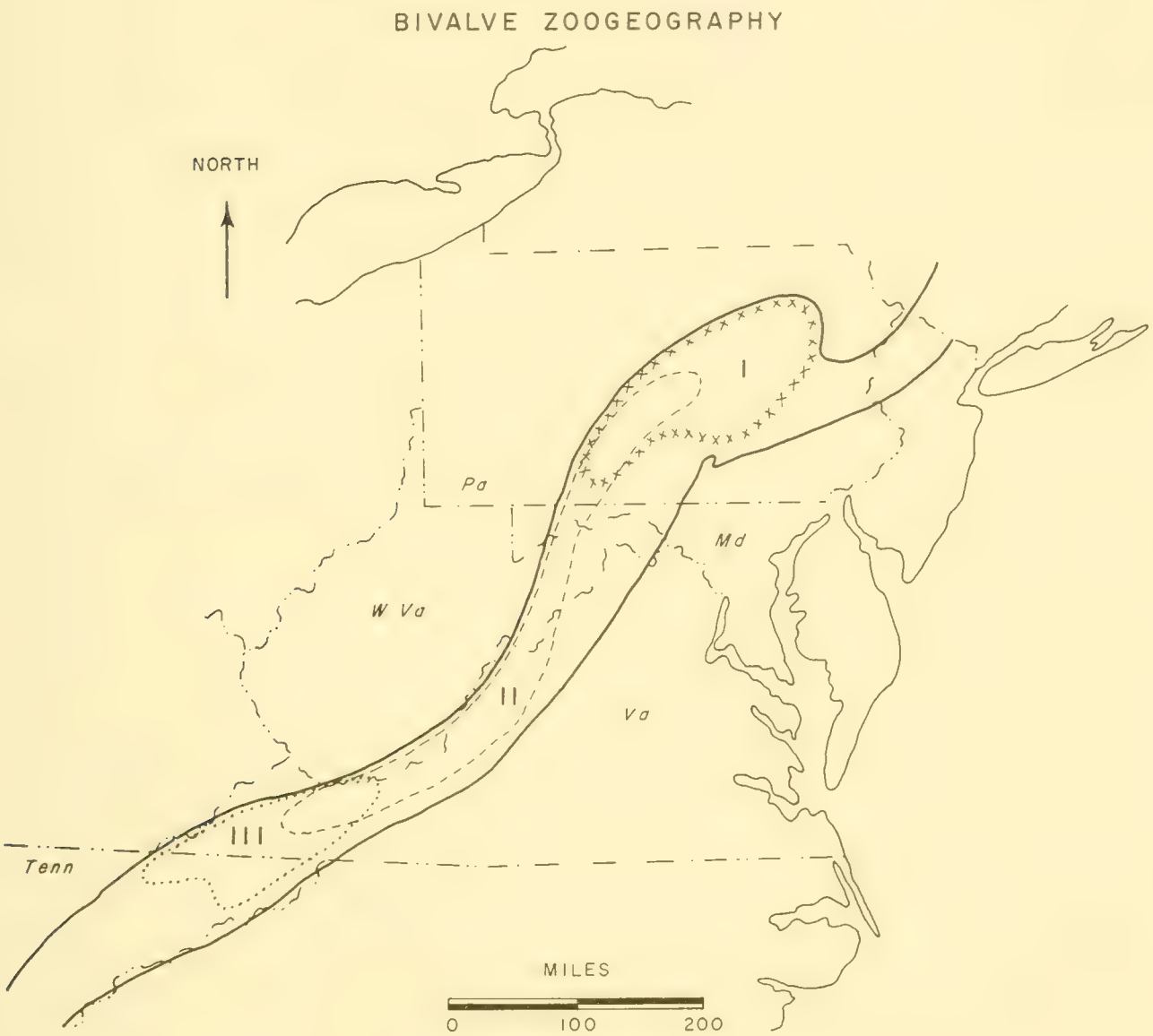


FIG. 17. A generalized outline of the distribution of the most common bivalve mollusc species in the central Appalachian Upper Ordovician. The three major bivalve faunal provinces are:

I. *Lyrodesma poststriatum*
Ambonychia radiata
Ctenodonta? pulchella
Praenucula levata

II. *Tancrediopsis cuneata*
Ambonychia praecursa
Modiolopsis modiolaris
Ischyrodonta truncata

III. *Pterinea (Caritodens) demissa*

Note as was the case with the brachiopod faunal provinces overlay may not indicate faunal mixing since the faunas are separated stratigraphically, see Fig. 18.

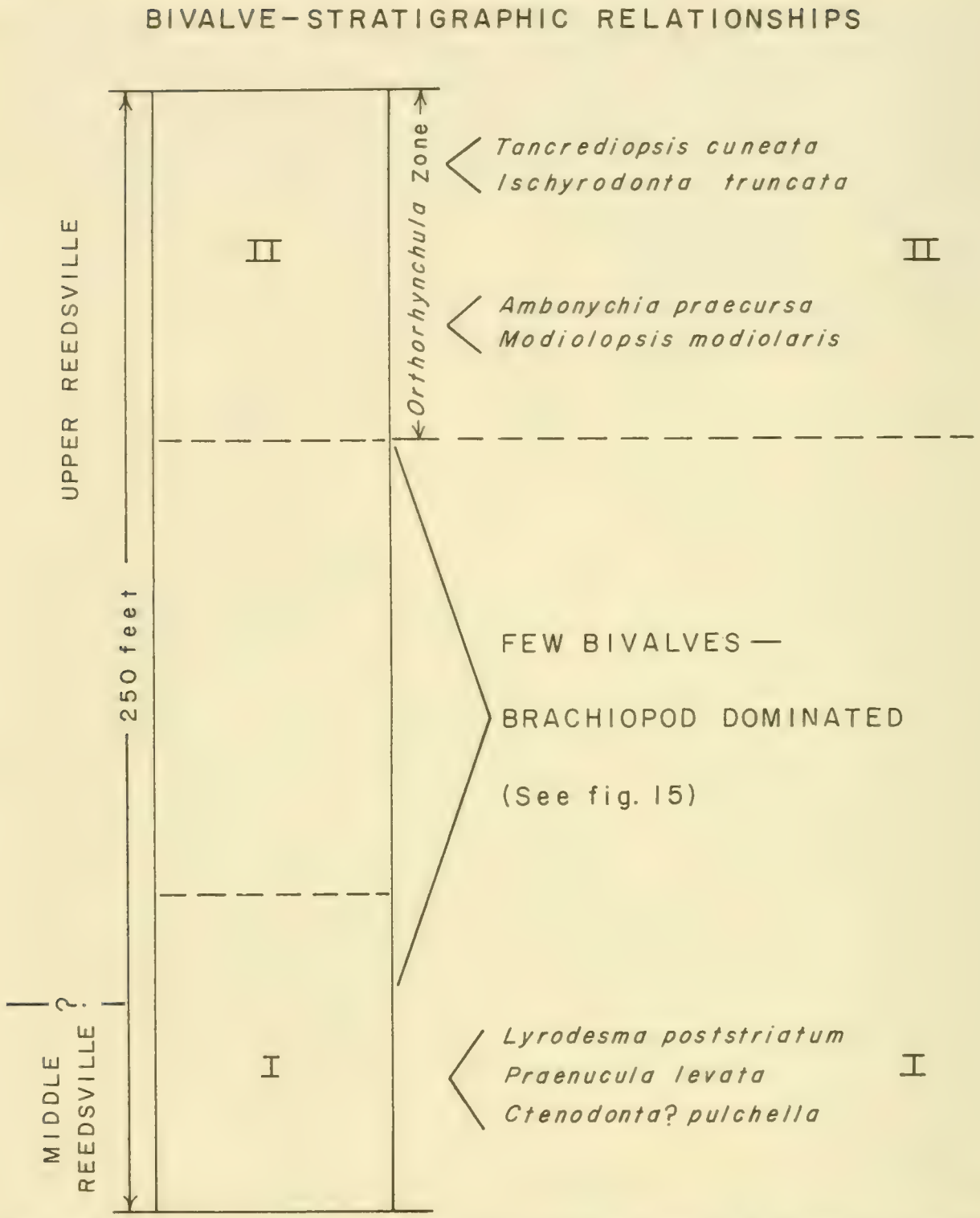


FIG. 18. A composite columnar section from the upper and middle(?) Reedsville in south-central Pennsylvania showing a pronounced stratigraphic-faunal separation of bivalve provinces I and II. See Figure 17 for geographic extent of this overlap.

bedding plane, in contrast to the much stronger association between *Ambonychia praecursa* and *Modiolopsis modiolaris*. There is a slight mixing of faunas of provinces II and III in southwestern Virginia, where there is no stratigraphic separation like that between I and II in the north. Bivalve province III is as restricted geographically as province I and shows no greater diversity, but the specimens are more numerous in a series of closely spaced localities. The two dominant species in province III, *Pterinea* (*Caritodens*) *demissa* and *Ambonychia cultrata*, exhibit no consistent stratigraphic separation.

TABLE 7. Bivalve faunal provinces. See also Fig. 17.

	Location	Abundant Fauna
I	Central Pennsylvania	*Lyrodesma poststriatum* *Praenucula levata* *Ctenodonta? pulchella*
II	South-central Pennsylvania to south-central Virginia	*Tancrediopsis cuneata* *Ambonychia praecursa* *Modiolopsis modiolaris* *Ischyrodonta? truncata*
III	Southwestern Virginia and northern Tennessee	*Pterinea (Caritodens) demissa* *Ambonychia cultrata*

PALEOAUTECOLOGY

Each of the twelve systematically segregated faunal provinces discussed in the preceding chapter was shown to be composed of normally less than four abundant genera and/or species. The important point is, however, that particular faunas do outline discernible zoogeographic patterns, and thus provide a basis for the interpretations of the life habits of each of the major taxonomic groups. Furthermore, understanding why these zoogeographic patterns exist in view of the autecology of the component species will provide for the recognition of probable environmental settings. Then by combining the ideas of zoogeography, autecology and the environmental setting, further interpretations of the structure of the Upper Ordovician faunal communities can be made. The discussion of the Upper Ordovician invertebrate communities will be reserved for the succeeding chapter.

BRYOZOA

The most important Bryozoa in the central Appalachian clastic facies are trepostomes, although there are rare fragments of cyclostomes and cryptostomes. Morphologically, the trepostomes are commonly ramose; the branches are either subcylindrical or lobate, flattened plates. The diameter of the lobations is not known to exceed 20 mm, and the cylindrical stems may be as thin as 1 mm. Irregular to hemispherical encrusting growth forms occur in a few localities but are never very numerous. Size differences in the diameters of the branches often may be of secondary taxonomic value at any one locality, but extrapolation of these data to nearby exposures was shown to be unreliable.

Comparison of the growth forms of the trepostomatous bryozoans with those of Recent bryozoans aids in reconstructing a probable environmental setting for these Upper Ordovician specimens. The most common Upper Ordovician clastic-facies forms are most like the Recent adeoniform and vinculariiform zoarial types (Stach, 1936; Lagaaij and Gautier, 1965)*. Lagaaij and Gautier (1965) have recognized these zoarial types off the Rhone delta and have found them widely distributed in 30 to 140 meters of water with mixtures of the two types in 50 to 80 meters of water, an area which can be generally classified as near the boundary between the inner and outer sublittoral — a quiet-water environment.

Lagaaij and Gautier (1965, p. 45) consider the correlation between depth and external morphological type primarily as a reflection of the sensitivity of the bryozoans

*Lagaaij and Gautier (1965, p. 51, text-fig. 24):
Adeoniform — zoarium erect, rigid, lobate, firmly attached to firm substratum. Vinculariiform — zoarium, erect, rigid, subcylindrical branches, attached to firm substratum.

to sedimentation rate. Maps of species numbers and diversity indicate that most Recent bryozoans are able to tolerate only very moderate to low rates of deposition, and therefore they are abundant only in quiet-water environments away from the delta fronts and inaccessible to sediment-laden currents. The common surface of attachment is a very slightly mobile sand-silt (Lagaaij and Gautier, 1965, p. 52). There is no reason to expect the Upper Ordovician forms to have been more tolerant of high sedimentation rates than modern forms. Recent bryozoans adopt an encrusting form when turbulence increases and the substratum becomes more mobile. Similarly, the Ordovician encrusting bryozoans are found in a coarser, better sorted sandstone. In some stratigraphic sections, increase in the silt/mud ratio is accompanied by a change from the ramose to the encrusting habit within the same genus (Fig. 30).

Generic diversity as related to sediment influx along the central Appalachian Late Ordovician shoreline is shown in Figure 19. Bryozoans are generally lacking in south-central Pennsylvania, Maryland and northern Virginia, the most probable source of

FIG. 19. A generalized outline of trepostomatous bryozoan diversity (genera) in the central Appalachian Upper Ordovician. Of particular note is that the low generic diversity in Pennsylvania, northern Virginia and eastern West Virginia may be directly related to the main source of terrigenous clastic influx during the Late Ordovician.

Numerals refer to number of genera identified at each locality where abundance of the individual genus was greater than 2 on the relative abundance scale.

a major Late Ordovician influx of terrigenous clastics. Immediately to the north and south of this source area, bryozoans are locally common and of the same genus in each locality. In southwestern Virginia and northern Tennessee, well away from the main terrigenous source, many localities have as many as five common genera. The obvious change in sediment type from sands and silts in the north to silty muds and muds in the south and the accompanying increase in bryozoan diversity probably indicate less turbulence and a lower rate of sedimentation in the south.

Figure 20* is a reconstruction of the probable environmental setting of the bryozoans during the Late Ordovician in the central Appalachians. *Dekayia* dominates the nearshore environments in the muddy silts and sands just off the main source area. *Hallopora* is abundant in many environments further offshore. With the increased diversity away from the area of clastic influx, there is a mixing of more bryozoan species, and the faunal composition of particular bryozoan populations is very unpredictable. A substratum of muddy silts or muds instead of coarser clastics is much preferred by the Upper Ordovician trepostomes; the diversity gradient may reflect a general gradient in the rates of sedimentation.

BRACHIOPODA

The interpretation of the life habits of the Upper Ordovician brachiopods is hindered by our lack of knowledge of the anatomy and ecology of modern brachiopods. Furthermore, there are no living representatives of the orthids, spiriferids and strophomenids, with the possible exception of the Recent genus *Lacazella* (see Elliott, 1965, p. H857). Some ecological speculations are possible, however, from both living brachiopods and from bivalve molluscs which show morphological and ecological convergence with the brachiopods.

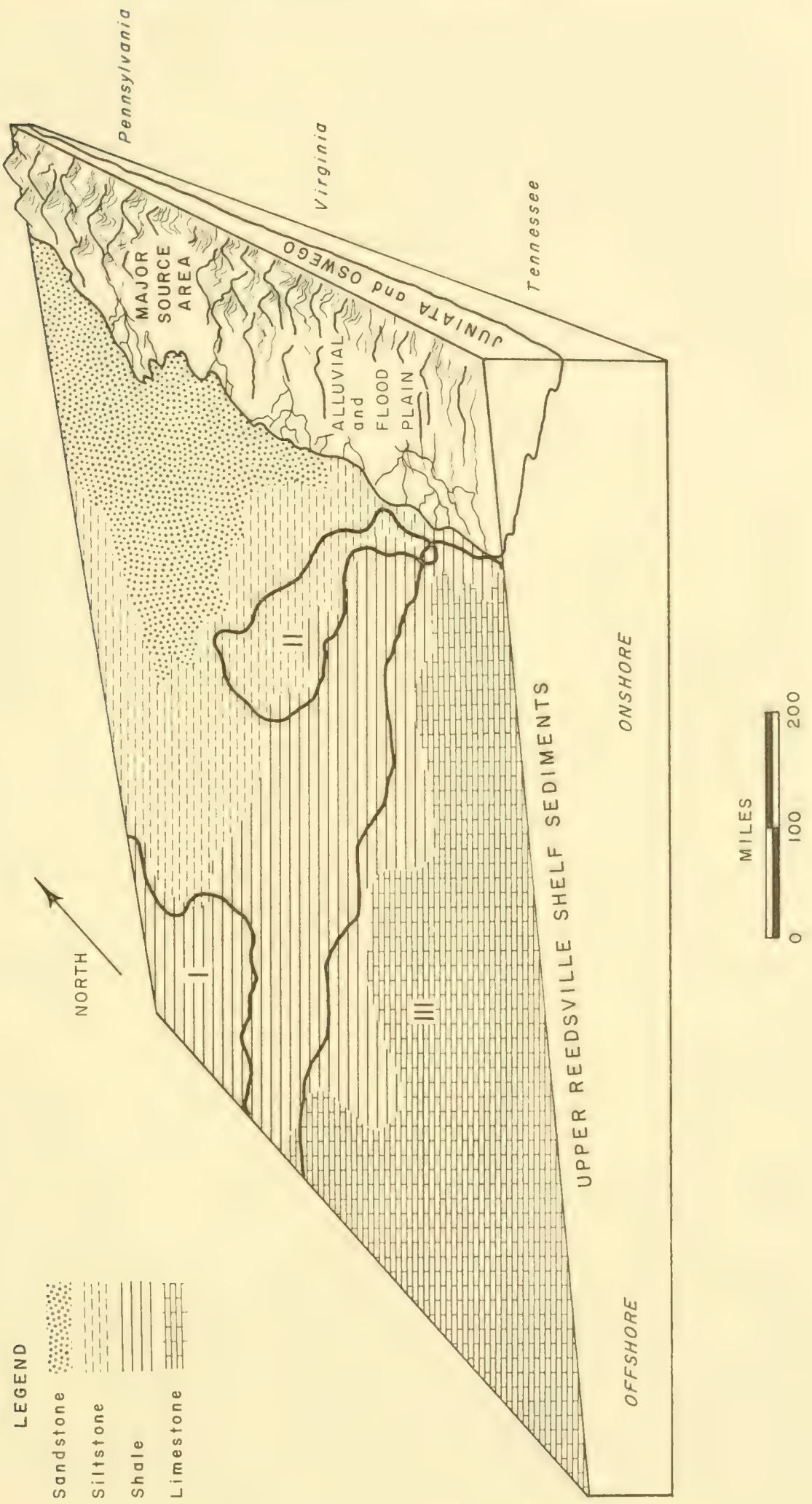
*Figures 20–23 are reconstructions of the probable onshore to offshore Late Ordovician environmental settings within each of the four major taxonomic groups based on the stratigraphic relationships (Figs. 15, 18), present zoogeographic distributions (Figs. 13, 14, 16, 17) and the Late Ordovician sedimentological framework of a prograding depositional regime (Fig. 12). Provincial boundaries as depicted in these figures are entirely interpretational and are not plots of collected distributional data.

FIG. 20. Reconstruction of the Late Ordovician bryozoan environmental setting in the central Appalachians. [See Fig. 13 which is an outline of bryozoan distribution (zoogeography) compiled directly from locality data without environmental interpretations.] This reconstruction, however, combines stratigraphic, sedimentological and ecological interpretations to form a general pattern of onshore to offshore environments occupied by abundant bryozoans. Genera abundant in these three bryozoan faunas:

I. *Hallopora*
II. *Dekayia*
III. *Monticulipora*
Amplexopora
Dekayia
Heterotrypa
Batostomella
Peronopora?
Hallopora

The scale refers to distance along the shore; onshore to offshore exaggeration is approximately ×4.

BRYOZOAN ENVIRONMENTAL SETTING



The study of the distribution of marine animals involves salinity, temperature, feeding type and substratum composition. All modern articulate brachiopods are limited to waters of normal marine salinity, and no fossil articulates are known from undoubted brackish-water deposits (Hyman, 1959, p. 520; Rudwick, 1965, p. H211); this indicates that all the central Appalachian Upper Ordovician species, except the linguloid species, were probably restricted to waters of normal marine salinity. By analogy with Recent linguloids, the occurrence of only numerous *Lingula*? probably reflects brackish-water conditions (Craig, 1952, p. 114). Its occasional mixture with *Orthorhynchula linneyi* probably indicates, however, other nearshore normally saline environments. *Lingula*? in the central Appalachians has not been found associated with any articulate brachiopod other than *Orthorhynchula linneyi.*

The sparse information concerning Ordovician paleotemperatures is of questionable significance. Spjeldnaes (1960), Opdyke (1962), Irving (1964) and Whittington (1966) have presented lithologic, paleomagnetic and faunal data in the reconstruction of the climatic zones and geography of the Ordovician. The paleomagnetic data presented by Irving (1964, p. 202), the evaporite-lithologic data of Opdyke (1962, p. 57, fig. 10) and the faunal data of Spjeldnaes (1960, p. 66, fig. 5A) and Whittington (1966, p. 730, fig. 16) are all consistent with a paleoequator that describes an arc bisecting the United States from Wisconsin to Texas. These data indicate a subtropical or warm temperate environment for eastern North America during the Late Ordovician. Whittington (1966, p. 731), working primarily with Ordovician trilobites, explains the extremely diverse Upper Ordovician faunas as reflecting the warmest of all Ordovician climates, probably responding to the direction and intensities of ocean currents much more than to substratum.

Recent brachiopods, with the exception of *Lingula,* appear to prefer cooler or deeper waters (Hyman, 1959, p. 594–599), but this may be a consequence of the general reduction in numbers, diversity, and bathymetric distribution of the phylum. The existence of local current patterns (McBride 1960, 1962) during deposition of the Martinsburg and Reedsville Formations must also be considered. Upwelling of colder, deeper basinal waters onto the Ordovician shelf and possible longshore currents could drastically influence the mean annual surface temperature patterns. Bayer (1967, p. 421), working with similar Mid-Continent Upper Ordovician orthid and strophomenid brachiopod faunas (cf. brachiopod faunal province I), considered the large number of individuals of relatively few species characteristic of cooler waters. We have little knowledge of the actual temperature and current controls that may have influenced the distribution of these central Appalachian Upper Ordovician brachiopods, although the central Appalachian shelf phosphates suggest a deep-water upwelling as the source of this phosphate.

Brachiopods are lophophorate suspension feeders. They do not filter in the same way as some of the filter-feeding bivalve molluscs, which sieve particles through their gill filaments. They feed by producing ciliary currents which bring a constant stream of water over the lophophore (Atkins, 1960; Atkins and Rudwick, 1962). Recent brachiopods are able to adjust the velocity of the feeding current by altering ciliary beat. Food gathering in brachiopods is more nearly equivalent to the filtering mechanism used by bryozoans, polychaetes, or crinoids. Food particles are perhaps removed from the water by trapping by a mucous layer on the lophophore (Chuang, 1956), but the mechanism of retention of food particles is not well understood (Jørgensen,

1966). There is apparently no sorting of the particles either according to shape or size (Jørgensen, 1966; for evidence of a different kind of sorting mechanism in fossil brachiopods see Ager, 1963, p. 58–59), or according to value as food (Rudwick, 1962; Hyman, 1959, p. 589–590).

To secure the optimum quantities of suspended organic matter, the mechanism of suspension feeding in the brachiopods may have required less current activity than necessary for the bivalves; therefore, differences in feeding methods may have resulted in the adaptation of brachiopods to life in areas where most epifaunal bivalve molluscs had been excluded. However, the rhynchonellid brachiopod *Orthorhynchula linneyi* is most abundant in an area where there are numerous mussel-like *Ambonychia praecursa, Modiolopsis modiolaris* and *Ischyrodonta truncata* nearby. The orthid *Hebertella sinuata* and the spiriferid *Zygospira recurvirostra* are also occasionally found with abundant *Pterinea* (*Caritodens*) *demissa* and locally abundant species of *Ambonychia* and *Modiolopsis*. Only the northern brachiopod fauna (faunal province I), dominated by the strophomenids *Rafinesquina "alternata"* and *Sowerbyella* (*Sowerbyella*) *sericea* and the dalmanellid *Onniella multisecta,* lacks an extensive epifaunal bivalve molluscan element. Here it is possible that the actual mechanisms of feeding, or a more efficient metabolism, of these brachiopod species could give them a selective advantage over the bivalves, but this is speculative.

The substratum, the only major environmental parameter for which we have any direct evidence in the central Appalachian Upper Ordovician, is particularly significant because of the sessile benthonic habit of the brachiopods. It appears that the nature of the substratum may have direct control over the pattern of brachiopod distribution, and also may determine the localization of species within the broader pattern of regional distribution. The rhynchonellids are most abundant in the coarse silts and sands. The strophomenids, dominant in the north, are more common in muddy silts, whereas the orthids, both in the north and in the south, appear in silty muds, muds and lime muds. The spiriferids show a preference for extremely fine sediments and are most abundant in the lime muds. Each of these brachiopods may also at times be found in other types of substratum. In addition, it appears that sedimentation rates and turbulence, as well as the substratum, play a major role in geographic distribution.

Rudwick (1965, p. H212) suggested that while brachiopods may tolerate moderate turbulence, they are less tolerant of actual sediment influx. Living brachiopods can interrupt the feeding process, adjust and reverse their ciliary beat to reject too large quantities of suspended particles and if necessary close their valves for several hours. Unlike some bivalve molluscs, they neither can maintain this complete shutdown for long periods nor (with the exception of linguoids) can they change their position if sedimentation becomes too rapid. According to Hyman (1959, p. 588) brachiopod powers of adjusting the feeding currents were a direct adaptation to life on "muddy" substratum where high turbidity occurs intermittently.

The segregation of the brachiopod faunas in the central Appalachian Upper Ordovician appears to be the result of the location and rate of the terrigenous clastic influx. The environmental setting of the brachiopods would begin at an early stage in the development of the source areas east of southern Pennsylvania and northern Virginia, when the clastic influx was low and the sedimentation rate low enough to permit the development of a major brachiopod shelf fauna, faunal provinces I

and III. With increased influx the shoreline prograded westward and distinct nearshore and offshore brachiopod components developed. *Lingula*? and *Orthorhynchula linneyi,* faunal province II, were more able to cope with the nearshore increase in terrigenous influx, but never thrived to the south in a presumably less turbid nearshore environment. The dominance of the nearshore faunas of province II reflects a dynamic change in the environmental conditions along the shoreline. Figure 21 is a representation of the environmental setting of the Late Ordovician brachiopod faunas during the development of the Oswego bar and barrier deposits in south-central Pennsylvania and eastern West Virginia.

The central Appalachian strophomenids, orthids and spiriferids probably lived in an environment where the average sedimentation rate was low, but where the sporadic occurrence of a high sedimentation rate probably took the form of sudden local turbidite flows. The brachiopods may have been able to adapt, to some extent, to these periodic sediment influxes, but localized populations may have been eliminated with subsequent repopulation from some other source. Recurrent orthid-strophomenid faunas in the Mid-Continent Upper Ordovician have been recently described by Bayer (1967). The orthid-strophomenid populations, decimated by increased rates of sedimentation, re-established themselves when sedimentation rates decreased. Since the central Appalachian linguloids and rhynchonellids existed in areas of high sedimentation, the possible vertical mobility of the linguloids was apparently an effective adaptation of *Lingula*?, but the morphological adaptations of *Orthorhynchula linneyi* are obscure. A long, stout pedicle and globose, sulcate form may have provided the necessary protection against complete annihilation of large segments of the population during periods of rapid sediment influx. Again the stratigraphic-sedimentological record seems to support an irregular rate of sedimentation. The transport of nearshore sands along the coast may have been sufficiently sporadic to permit the establishment of large rhynchonellid populations. The morphological adaptations of individual species are considered in more detail in the systematic discussion of each taxon.

Hyman (1959, p. 591) stated that no combination of species of Recent brachiopods has been shown to recur in a predictable way in Recent level-bottom associations, although as sessile animals the brachiopods would be expected to have some common associations with other sessile, sedentary animals. Like most modern brachio-

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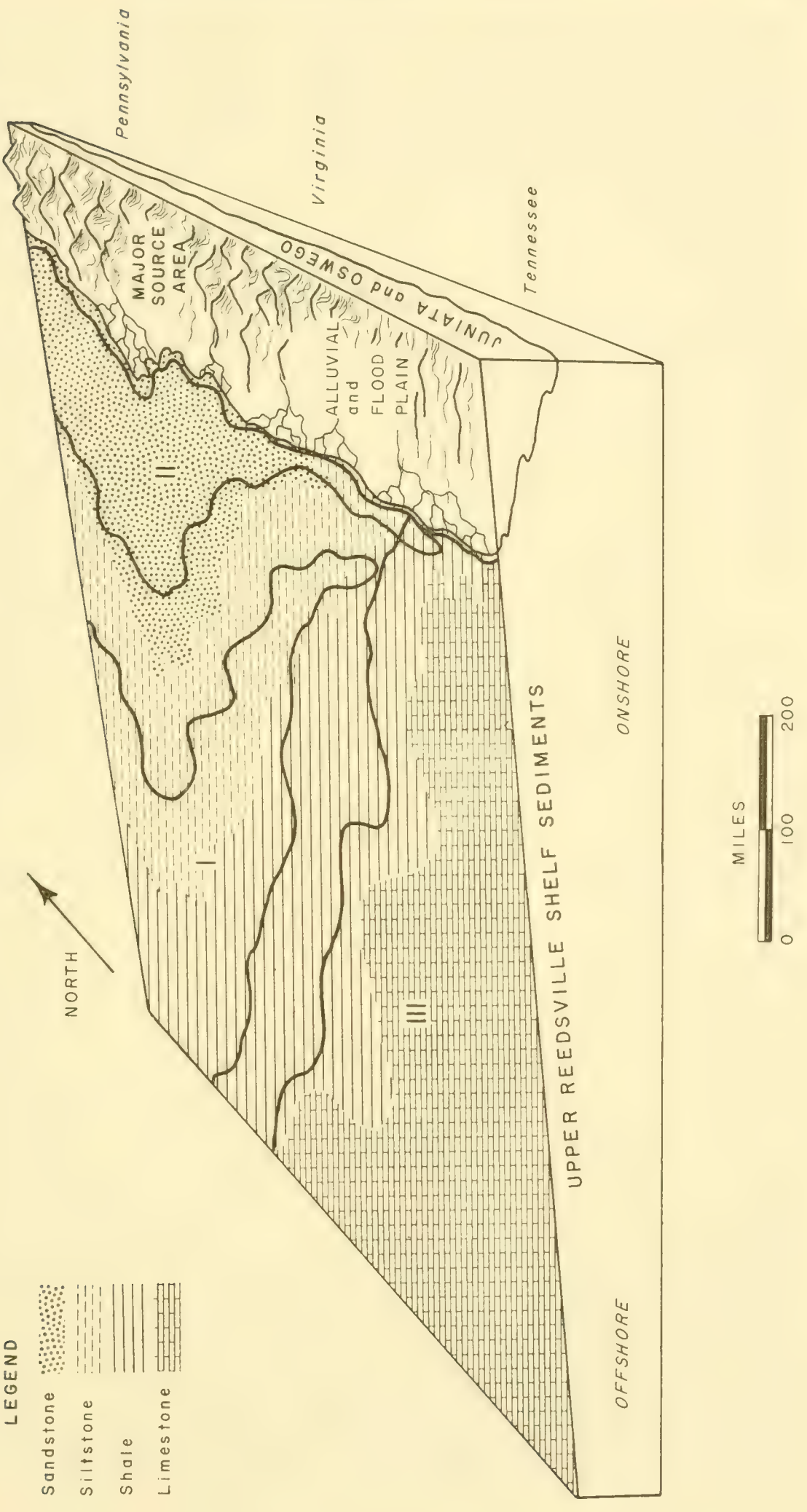
FIG. 21. Reconstruction of the Late Ordovician brachiopod environmental setting in the central Appalachians. [See Fig. 14 which is an outline of brachiopod distribution (zoogeography) compiled directly from locality data without environmental interpretations.] This reconstruction, however, combines stratigraphic, sedimentological and ecological interpretations to form a general pattern of onshore to offshore environments occupied by abundant brachiopods. Species abundant in these three brachiopod faunas:

I. *Rafinesquina "alternata"*
Sowerbyella (Sowerbyella) sericea
Onniella multisecta
Zygospira modesta
II. *Orthorhynchula linneyi*
Lingula?
III. *Zygospira recurvirostra*
Hebertella sinuata

The scale refers to distance along the shore; onshore to offshore exaggeration is approximately ×4.

BRACHIOPOD ENVIRONMENTAL SETTING



pods, the central Appalachian Upper Ordovician forms appear to have been gregarious (see Mattox, 1955, for a Recent example). Recent brachiopods have a pelagic larval stage that lasts only a few hours. Although it appears that the powers of larval dispersal are limited (Hyman, 1959, p. 590; Rudwick, 1965), I doubt that the vagaries of larval settling alone could account for the absence of a species from an apparently suitable substratum.

GASTROPODA

An interpretation of the life habits and environmental setting of the Upper Ordovician bellerophontacean and pleurotomariacean gastropods can be made by inference from the Recent Pleurotomariacea; there are no living Bellerophontacea. Batten (1958, p. 169) and Yochelson (1960, p. 215) reviewed the sparse ecologic data, derived mainly from the work of Yonge (1947), dealing with pleurotomariaceans. Archaeogastropods require a firm substratum and low turbidity. Their bipectinate, aspidobranch gills are easily fouled because their ciliary action is not capable of freeing quantities of mud from the gill filaments. Batten (1958) also noted that the majority of recent Pleurotomariacea live at depths between 50 and 200 fathoms and seem better adapted to colder, possibly deeper waters with some, however, tolerating brackish-water conditions. All are presumably macrophagous herbivores, browsing on algal fronds or collecting algal material from the substratum surface (Graham, 1955, p. 149).

The Upper Ordovician pleurotomariacean gastropods, faunal province I, are most abundant in fine sandstones and siltstones. The stratigraphic and sedimentological evidence indicates that they existed farther from shore than the bellophontaceans of faunal province II. The characteristic local patchiness of province I species may reflect the irregular distribution of detrital plant material by gentle currents moving over the substratum. Since the influence of water temperature is difficult to ascertain, I find it difficult to attribute the distribution of *Loxoplocus* (*Lophospira*) solely to current patterns.

The most abundant bellerophontid gastropod, *Plectonotus*? sp. of faunal province II, is found in the area where the upper Reedsville silts and sands are transitional upward into the cross-bedded sands and organic-rich muds of the lower Oswego. *Plectonotus*? sp. is not commonly associated with the pleurotomariaceans, though both types of gastropods inhabit silts of the same general texture. Seemingly this combination of Reedsville-Oswego lithologies could be a major influence on the distribution of abundant plectonotid species. The organic-rich black muds of the lagoons may be protected areas of Ordovician algal stands; the browsing of the bellerophontid on the algal fronds would probably place it above any sporadic turbid currents which would tend to clog its delicate ctenidia. The low pH of the organic-rich muds probably prevented the preservation of the calcareous shells of this species, if indeed they did inhabit this region; but shells were preserved farther off-shore, clumped together and often surrounded by a sediment with more organic matter than the surrounding rock. *Plectonotus*? sp. could have been rafted out into the deeper marine waters on algal fronds during periods of high water, or even have been maintained on a firm substratum if there had been an adequate supply of plant

detritus near the site of preservation. The patchiness or clumping of the bellerophontids, which is also characteristic of the pleurotomariaceans, could result from a highly localized food source, such as algal material concentrated in shallow basins or hollows between shoals. These also appear to be the areas of the highest concentration of phosphate grains, many forming as internal molds of *Plectonotus*? sp.

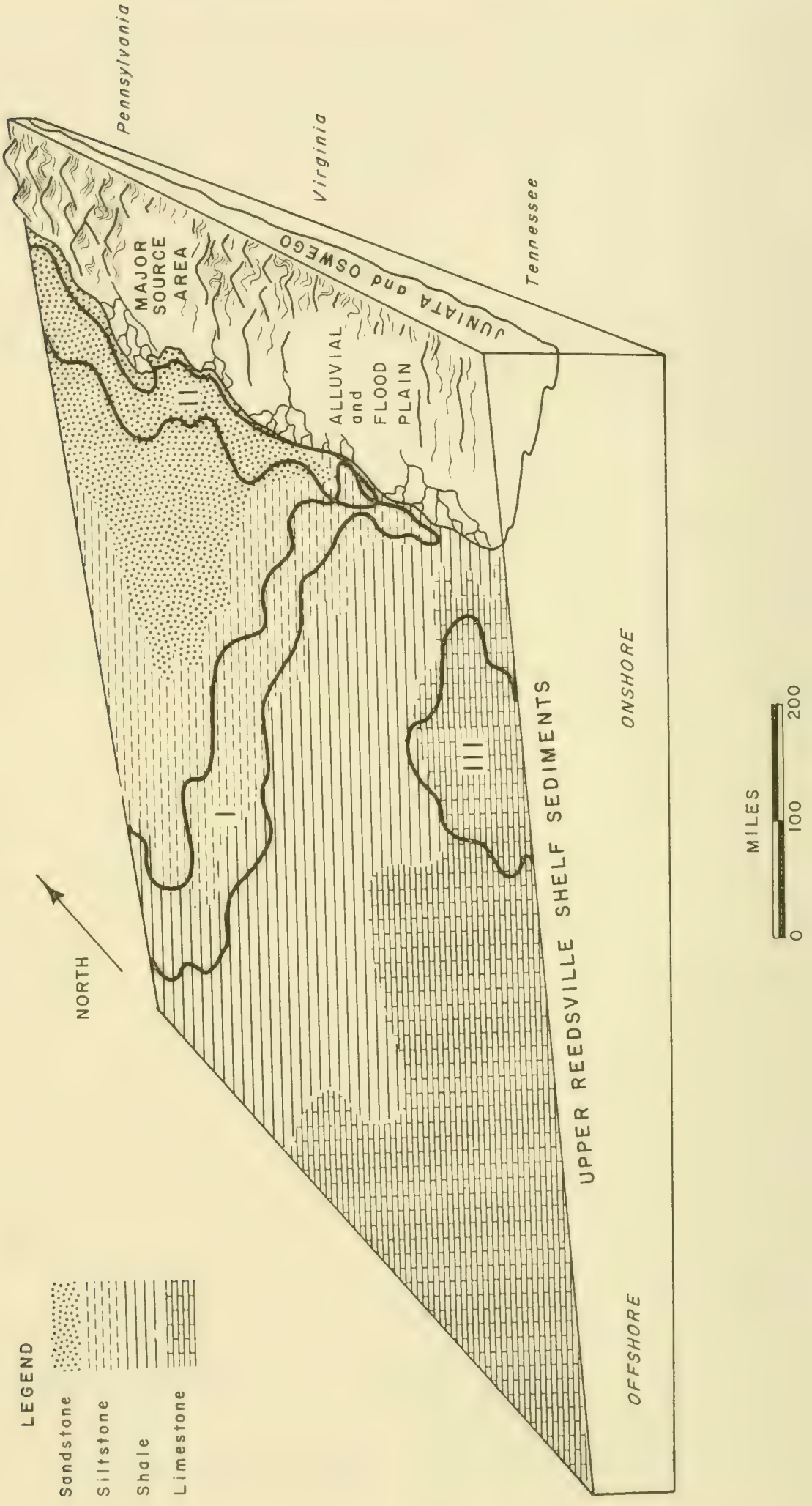
In faunal province III the murchisoniid gastropods are confined exclusively to the Upper Ordovician carbonate muds of northern Tennessee, in contrast to the silty substratum of the bellerophontid and pleurotomariid provinces to the north. Figure 22 reconstructs the environmental setting of the gastropod fauna along the Late Ordovician central Appalachian shoreline. Cox and Knight (1960, p. I290) describe murchisoniid morphology. These snails have the inhalant siphon characteristic of the mesogastropods, although they retain features characteristic of the archaeogastropods. Recent Pleurotomariacea can exist only in clear waters and on a firm substratum. As Lower Paleozoic pleurotomariacean populations gradually expanded onto a muddier substratum, individuals possessing a ctenidial structure from which mud particles could be more easily removed would have had a selective advantage over those individuals whose powers of removing mud particles from the ctenidia was limited. Along with the development of monopectinate ctenidia, evolutionary changes advantageous to the mud dweller would be the development of an extensible inhalant siphon and the modification of the foot to allow the ancestral mesogastropod to move through or over the soft substratum. Thus the clear separation of the northern bellerophontid and pleurotomariid gastropod faunas from the southern murchisoniid gastropods was probably influenced by substratum type.

BIVALVIA

The life habits and environmental setting of the central Appalachian Upper Ordovician bivalves may be inferred by comparison with analogous modern bivalve families. Recent nuculoids, mussels and pterioids give some clues as to the ecology of the Upper Ordovician species, but uncertainties exist because only a few Recent studies have gathered enough data for an adequate reconstruction of ancient autecology. Also, some abundant central Appalachian Upper Ordovician bivalve genera — for example, *Lyrodesma*—permit few comparisons with any known Recent species. As pointed out in the discussion of the Brachiopoda, four of the most critical factors controlling the distribution of marine animals are salinity, temperature, feeding type and substratum. These environmental variables, singly or in combination, control the distribution of fossil and Recent Bivalvia.

Most Upper Ordovician bivalve species appear to have lived in waters of normal marine salinity, as they either are associated with species that are commonly accepted as being normally marine (e.g., articulate brachiopods) or have Recent morphological analogues that live in waters of normal marine salinity. One possible euryhaline species is the nuculoid *Tancrediopsis cuneata*, which commonly occurs with numerous specimens of *Lingula*? in the upper parts of the upper Reedsville Formation (see Figs. 7 and 29). Here the upper Reedsville muddy siltstones and sandstones are interbedded with the bar-barrier deposits of the Oswego-like sandstones. *Tancrediopsis cuneata* may have been able to tolerate periods of fresh-water influx and

GASTROPOD ENVIRONMENTAL SETTING



accompanying changes in salinity. Parker (1960, p. 310) lists two species of *Nuculana,* a Recent nuculoid, as occurring in an enclosed lagoonal environment along a considerable length of the northern coast of the Gulf of Mexico. *Nuculana* was found on both sides of the prograding Mississippi deltaic complex and apparently is tolerant of changes in salinity, temperature, and substratum type. The central Appalachian *Tancrediopsis cuneata* could also have been adapted to a variety of environmental conditions; it is found in sediment types ranging from muds to silts and shows a considerable north-south distribution on both sides of the area of maximum terrigenous influx. The only other possible exception to a normal marine existence may be found in the few isolated patches of abundant *Modiolopsis modiolaris* along the eastern exposures of the Reedsville Formation in central Virginia. These Upper Ordovician mussel-like bivalves may have occupied an intertidal silt-mud flat situation like that inhabited by the related *Modiolus rectum,* a common species along the west coast of the United States.

Temperature is also likely to have controlled the distribution of the central Appalachian Upper Ordovician Bivalvia, but evidence for temperature variations is indirect. Kinne (1963), Read (1964) and Hall (1964) have reviewed and summarized a great deal of information pertaining to the distribution and physiological adaptations of the modern bivalves as a function of temperature. Hutchins' (1947) classic paper outlines the strict temperature tolerances that exist in Recent shelf invertebrates. Well-defined latitudinal boundaries of particular associations of Recent bivalves have proved extremely useful in ecological interpretations of Tertiary and Quaternary bivalves. Woodring, Bramlette and Kew (1946), Durham (1950) and Valentine (1961) have shown distinct isothermal control of the distribution of species through time. The north-south temperature gradient of the Upper Ordovician has been surveyed in the discussion of brachiopod life habits, and it appears that the central Appalachian Upper Ordovician shoreline was located somewhere between 10 and 20 degrees of latitude with reference to the paleoequator (see Opdyke, 1962, p. 57, fig. 10), a subtropical or warm temperate environment.

Temperature control of the Upper Ordovician Bivalvia may have been effected either by local current patterns or by a broader onshore-offshore change in temperature. Local current patterns have been documented from previous sedimentological studies in the Reedsville and Martinsburg Formations (McBride, 1960, 1962) and

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FIG. 22. Reconstruction of the Late Ordovician gastropod environmental setting in the central Appalachians. [See Fig. 16 which is an outline of gastropod distribution (zoogeography) compiled directly from locality data without environmental interpretations.] This reconstruction, however, combines stratigraphic, sedimentological and ecological interpretations to form a general pattern of onshore to offshore environments occupied by abundant gastropods. Species abundant in these three gastropod faunas:

I. *Loxoplocus* (*Lophospira*) *abbreviata*
L. (*L.*) *perangulata*
L. (*L.*) *ventricosta*
Ruedemannia? *lirata*
Sinuopea?
II. *Plectonotus*? sp.
Bucania sp.
III. *Murchisonia*?

The scale refers to distance along the shore; onshore to offshore exaggeration is approximately ×4.

could result from colder upwellings along the shelf. The sharp separation of the species of faunal provinces I and II may reflect an onshore-offshore temperature gradient. The species of faunal province I appear, from stratigraphic and sedimentological evidence, to occupy an outer sublittoral environment; the characteristic patchy distribution of *Lyrodesma poststriatum* may reflect localized colder currents on the shelf. The species in faunal provinces II and III, predominantly inner sublittoral types, may have adapted to a less localized, longshore, warmer isothermal pattern that extended almost the entire length of the central Appalachains. Figure 23 is a diagram of the bivalve species as they were probably distributed during the development of the Oswego bar and lagoonal deposits.

The three main feeding types of most Recent species of Bivalvia are: infaunal deposit or detritus feeders, epifaunal suspension feeders, and infaunal, usually siphonate, suspension feeders. All three feeding types are represented in the central Appalachian Upper Ordovician. Epifaunal suspension feeders dominate the Upper Ordovician, whereas an infaunal suspension feeding habit, which is very common in Recent bivalves, probably existed in only one species, *Lyrodesma poststriatum* (Table 8). The infaunal deposit feeding habit is summarized in a paper by Yonge (1939) on the Recent protobranch bivalves. The Recent genera *Nucula* and *Solemya* correspond very closely to the Ordovician *Tancrediopsis cuneata*, *Ctenodonta? pulchella*

TABLE 8. Upper Ordovician Bivalve Feeding Types

Infaunal		Epifaunal
Deposit	Suspension	Suspension
Tancrediopsis cuneata[2]	*Lyrodesma poststriatum*[1]	*Ambonychia praecursa*[2]
Praenucula levata[1]		*Modiolopsis modiolaris*[2]
Ctenodonta? pulchella[1]		*Ischyrodonta truncata*[2]
		Ambonychia cultrata[3]
		Pterinea (Caritodens) demissa[3]

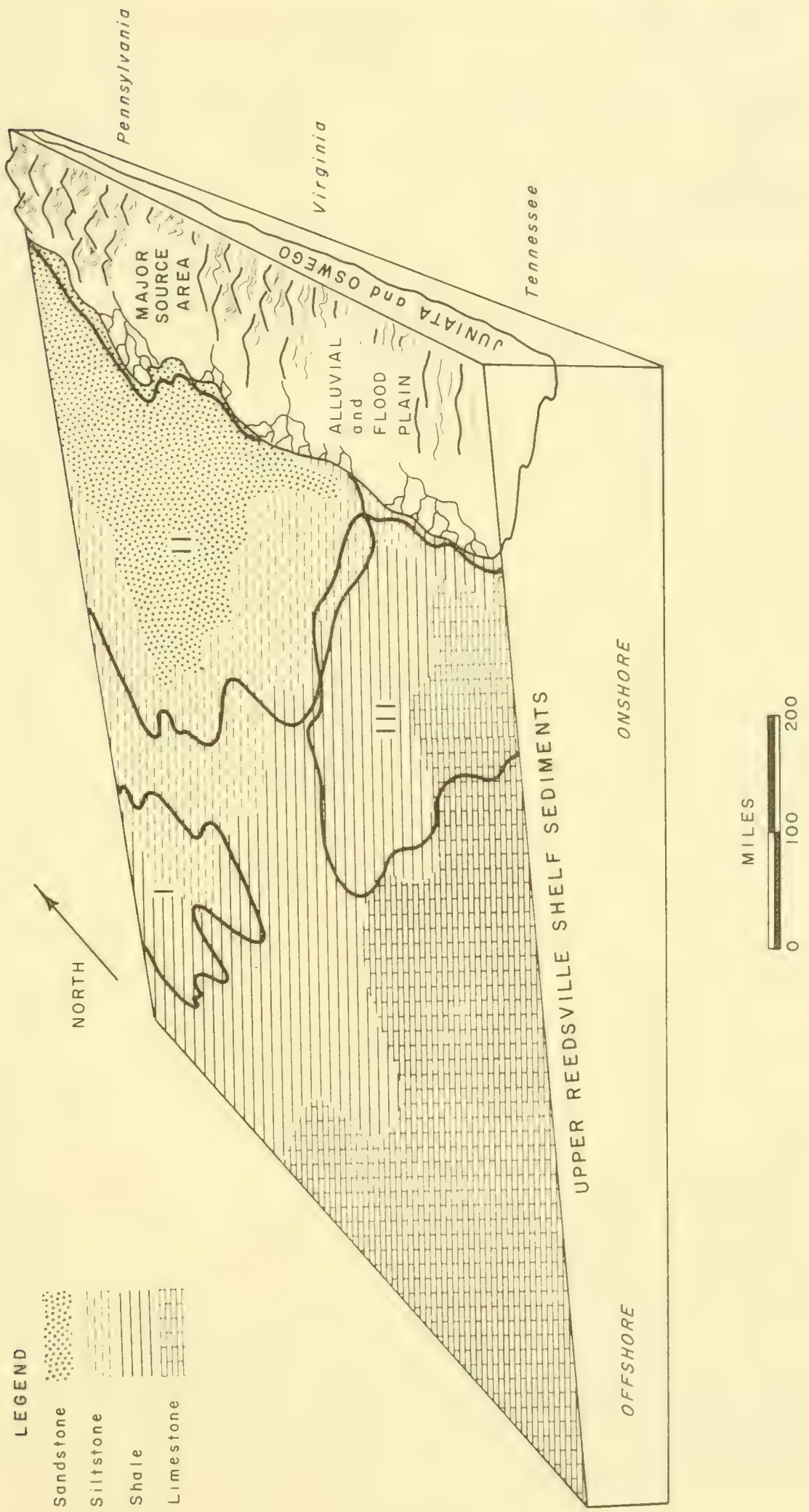
Numbers refer to bivalve faunal provinces (Fig. 17); 1 = offshore, 2 and 3 = onshore. This chart of Upper Ordovician bivalve feeding types emphasizes the fact that bivalve associations are dominated by either infaunal deposit feeders or epifaunal suspension feeders. A reconstruction of the bivalve environmental setting (Fig. 23) shows a pronounced increase in the numbers and diversity of infaunal species from onshore to offshore.

FIG. 23. Reconstruction of the Late Ordovician bivalve environmental setting on the central Appalachians. [See Fig. 17 which is an outline of bivalve distribution (zoogeography) compiled directly from locality data without any environmental interpretations.] This reconstruction, however, combines stratigraphic, sedimentological and ecological interpretations to form a general pattern of onshore to offshore environments occupied by abundant bivalve molluscs. Species abundant in these three bivalve faunas:

I. *Lyrodesma poststriatum*
Praenucula levata
Ctenodonta? pulchella
II. *Ambonychia praecursa*
Modiolopsis modiolaris
Tancrediopsis cuneata
Ischyrodonta truncata
III. *Ambonychia cultrata*
Pterinea (Caritodens) demissa

The scale refers to distance along the shoreline; onshore to offshore exaggeration is approximately ×4.

BIVALVE ENVIRONMENTAL SETTING



and *Praenucula levata*; all of these were presumably deposit feeding bivalves. They occupy a number of diverse environments, as do Recent nuculoid species. The few *Nuculites* found in the central Appalachian Upper Ordovician are also members of the infaunal deposit feeding group, but more closely resemble the Recent genus *Nuculana.*

Epifaunal suspension feeders, dominant in the central Appalachian Upper Ordovician, represent the most important type of bivalve feeding in early Paleozoic time. Though epifaunal suspension feeding bivalves are numerically somewhat less important today than infaunal ones, the feeding habits of various species of *Crassostrea, Ostrea* and *Mytilus* have been carefully studied. Graham (1949) summarized many of the bivalve feeding types and supplemented the previously reported data with his analysis of the contents of the bivalve stomach. The effects of various types and concentrations of micro-organisms on the feeding habits and pumping abilities of the epifaunal suspension feeders have been the subject of a few recent investigations (Davids, 1964), but the data is incomplete and of only limited use. There are numbers of epifaunal Bivalvia in the Lower Paleozoic living with some abundant brachiopod species and seemingly in direct competition with the Brachiopoda, which feed similarly. The possible adaptive advantages of the Bivalvia which allowed them to dominate the nearshore, more turbulent environments or, conversely, those which may explain the superiority the Brachiopoda had over the epifaunal Bivalvia in quieter sublittoral environments are not known (Figs. 21 and 23 show the offshore area limitations of the Bivalvia as compared to the Brachiopoda). Brachiopod diversity increases noticeably in the less turbulent, presumably offshore waters, whereas the epifaunal suspension feeding bivalves are much more diverse in a current-influenced, nearshore environment. Mechanisms for dealing with a shifting substratum thus may have been more effective in the Bivalvia than in the Brachiopoda, something that needs further study in modern environments.

The infaunal suspension feeder, a very important feeding type in many Recent environments, is rare in the Lower Paleozoic and is represented only by *Lyrodesma poststriatum* in the central Appalachian Upper Ordovician. The presence of the pallial sinus in the genus *Lyrodesma* was first figured by Ulrich (1893, pl. 47, fig. 9), and I have collected specimens from the central Appalachians that show an equally well-defined sinus. The evolutionary significance of this scattered, but locally abundant, infaunal siphonate bivalve is uncertain. It seems very likely, however, that *Lyrodesma* did not give rise to the later prolific siphonate fauna, but was rather a short-lived offshoot with no descendants. Newell (1965, p. 19) lists the Family Lyrodesmatidae as a questionable member of the trigonids, and Babin (1966, p. 304, fig. 26) shows *Lyrodesma* as a possible ancestor of the genus *Modiolopsis.* But both these interpretations appear to be unlikely with recognition of the distinct pallial sinus.

The central Appalachian Late Ordovician substratum is the major environmental parameter for which direct evidence is available. Recent studies have stressed the importance of a suitable substratum for the settling of pelagic larvae of benthic invertebrates (Wilson, 1952; Thorson, 1957); and Purdy (1964) summarized the abundance, diversity and distribution of marine invertebrates as a function of substratum type. Carey (1965), working off the coast of Oregon, Sanders (1958) in Buzzards Bay, and Craig and Jones (1966) in the Irish Sea have demonstrated the close correlation between the diversity and abundance of epifaunal and infaunal

invertebrates, including bivalves, as related to substratum. Generally, infaunal deposit feeders are most common in the more organically rich, finer-grained sediments. The coarser silt and sand environments are dominated by epifaunal suspension feeders. As Carey (1965, p. 100) has stressed, although there is always a complex of factors at work, particle size of sediment generally decreases with distance from shore, with an accompanying increase in the number of deposit feeding organisms. Savilov (1959), working in the northern Okhotsk Sea, found that a replacement of one feeding type by another was related to distance from shore and substratum type. In the Ordovician, the substratum differences probably account for some of the patterns of bivalve distribution in certain parts of the central Appalachians. The changes in the bivalve species among the three faunal provinces interpreted in the light of these Recent distributions are as follows: The epifaunal suspension feeders dominate the silt and muddy silt nearshore environments, but there is a noticeable decrease in numbers and diversity from province II to province III, with an accompanying decrease in the particle size of the sediment. The presumably offshore faunal province I, abundant in the fine silts and muds, shows a higher percentage of infaunal detritus feeders than the other two nearshore provinces. Savilov (1959) states that in Recent environments suspension feeders predominate in shallow waters whereas infaunal detritus feeders dominate offshore muddy silts.

Thus it can now be shown that the twelve systematically segregated faunal provinces each contain species that are not only ecologically compatible within the provinces themselves, but also provide evidence for the definition of distinct marine shelf environments. These environmental interpretations are consistent for those bryozoan, brachiopod, gastropod and bivalve faunal provinces that are superposed without stratigraphic separation (Figs. 20-23; refer also to Figs. 13, 14, 16 and 17). Furthermore this allows for the synthesis of this data into benthic marine communities that are composed of a variety of taxonomic groups and that occupied particular environmental regimes. The following chapter considers this provincial synthesis.

APPALACHIAN UPPER ORDOVICIAN FOSSIL COMMUNITIES

In the preceding discussion of zoogeography and autecology of the Upper Ordovician faunas it is evident that systematically segregated bryozoan, brachiopod, gastropod and bivalve faunas are not isolated from one another, but rather are closely interrelated geographically and stratigraphically. Consistent and recurrent associations of species among the twelve faunal provinces has led to the recognition of three main faunal associations, termed communities; these are outlined in Table 9. Two numerically less significant taxa, the crinoids and trilobites, are also included in Table 9, though neither of these taxa has been treated in detail in this study.

The three communities are composed of groups of species, all of which show a high degree of affinity and a pronounced tendency to recur together throughout the Upper Ordovician strata (Table 3; the recurrences are based on those species which show a relative taxonomic density index of 3 or more). This consistent association of certain species was the basis of Petersen's (1914) concept of a marine bottom community, a concept which is accepted by most marine ecologists today (see Jones, 1950; Thorson, 1957; Valentine, 1961; Fager, 1963; and Speden, 1966), and was employed by Johnson (1962) in his study of Mid-Continent Pennsylvanian assemblages. Each Late Ordovician community is named for its most conspicuous and co-dominant species. The communities are as follows (the specific designation is omitted throughout the remainder of the text):

1. *Sowerbyella sericea–Onniella multisecta* Community
2. *Orthorhynchula linneyi–Ambonychia praecursa* Community
3. *Zygospira recurvirostra–Hebertella sinuata* Community

The communities are subdivided into seven multi-species populations, also on the basis of consistent species associations and recurrence (see again Table 3; as before, the species considered in the recurrence are those whose density index is 3 or more at any one locality). The communities and populations are similarily defined but the latter are more restricted geographically and stratigraphically; clustering of particular species takes place within the overall community structure and is believed to reflect more localized environmental conditions. Table 10 outlines the seven multi-species populations composing these three Late Ordovician communities. The populations are:

TABLE 9. The Late Ordovician Faunal Communities: *Sowerbyella–Onniella*, *Orthorhynchula–Ambonychia*, and *Zygospira–Hebertella*, each based on a recurrent association of the species listed. (See also Table 3).

Faunas	Bryzoans	Brachiopods	Gastropods	Bivalves	Trilobites	Crinoids
Sowerbyella–Onniella Community	*Hallopora*	*Rafinesquina "alternata"*	*Loxoplocus (Lophospira) abbreviata*	*Lyrodesma postriatum*	*Isotelus*	crinoid columns
		Sowerbyella sericea	*L. (L.) perangulata*	*Praenucula levata*	*Flexicalymene*	
		Onniella multisecta	*L. (L.) ventricosa*	*Ctenodonta? pulchella*	*Cryptolithus*	
		Zygospira modesta	*Sinuopea?*			
			Ruedemannia? lirata			
Orthorhynchula–Ambonychia Community	*Dekayia*	*Orthorhynchula linneyi*	*Plectonotus?* sp.	*Tancrediopsis cuneata*	Very rare	Very rare
		Lingula?	*Bucania* sp.	*Ambonychia praecursa*		
				Modiolopsis modiolaris		
				Ischyrodonta truncata		
Zygospira–Hebertella Community	*Monticulpora*	*Hebertella sinuata*	*Murchisonia?*	*Pterinea (Caritodens) demissa*	Very rare	Very rare
	Dekayia	*Zygospira recurvirostra*		*Ambonychia cultrata*		
	Batostomella					
	Amplexopora					
	Hallopora					
	Heterotrypa					
	Peronopora?					

Sowerbyella–Onniella Community
- Strophomenid Population
- Orthid-Crinoid Population

Orthorhynchula-Ambonychia Community
- Linguloid Population
- Rhynchonellid Population
- Modiolopsid Population

Zygospira-Hebertella Community
- Spiriferid Population
- Orthid Population

It is important to emphasize that the definition of communities and populations is quite distinct from that of the systematically segregated faunal provinces. The bryozoan, brachiopod, gastropod and bivalve faunal provinces occupied distinct geographic areas within the central Appalachians and were strictly defined by the presence or absence of a particular fauna, whereas the Late Ordovician communities are composed of numbers of recurrent species, one or more of which may be absent or rare at a given locality within the area occupied by the community.

The areal distribution of the three communities throughout the Upper Ordovician is shown in Figure 24. This is not a reconstruction based on the stratigraphic or sedimentological framework, but rather a plot of the collected data for each central Appalachian exposure. These data can further be viewed stratigraphically, as presented in Figure 6. It cannot be overemphasized that both geographic and stratigraphic presentations are based solely on the association and recurrence of the abundant Upper Ordovician species. Figure 6 also details the stratigraphic distribution of the seven multi-species populations. The biofacies relationships of these populations are the basis for a reconstruction of the faunal distribution along the central Appalachian Late Ordovician shelf.

Figure 25 is a reconstruction of the onshore to offshore community distribution based on stratigraphic relationships (Fig. 6), present geographic distribution (Fig. 24), autecological interpretations of the individual faunas (Figs. 20-23) and the Late Ordovician sedimentological framework of a prograding depositional regime (Fig. 12). Figures 26 and 27 are profiles taken across this reconstructed central Appalachian Late Ordovician shelf, showing the inferred distribution of the abundant faunal elements (see also Figs. 10 and 11, showing Late Ordovician depositional environments). These figures emphasize the pronounced nearshore to offshore change in abundant faunas, although there is considerable mixing and overlap of the individual species. In Figure 28 the diversity of the preserved Late Ordovician shelf fauna is contoured. The low diversity of nearshore and offshore environments, although documented in the Late Ordovician only by those animals preservable as fossils, is also characteristic of Recent environments. The Late Ordovician nearshore low count (C in Fig. 28) was probably caused by salinity, temperature and desiccation stress conditions in the lagoonal and tidal flat environments of the upper Reedsville and lower Oswego strata, and by shifting substratum along the margins of the lower Oswego bars and barriers. The offshore low diversity (C′ in Fig. 28) found only in the north, represents predominantly a trilobite fauna not examined in detail, and is common in the lower Reedsville gray-black muds; it appears to reflect, by analogy with

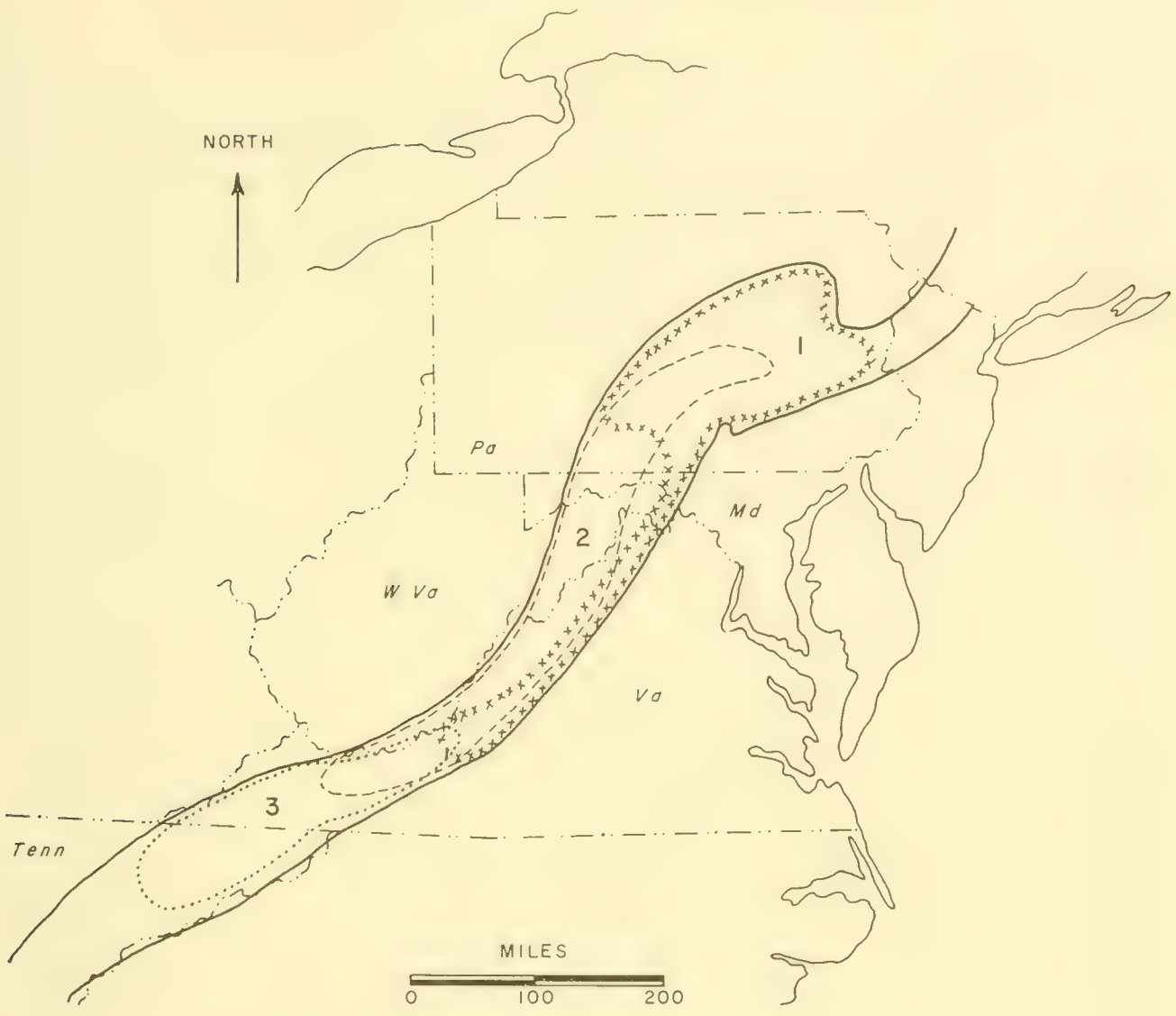


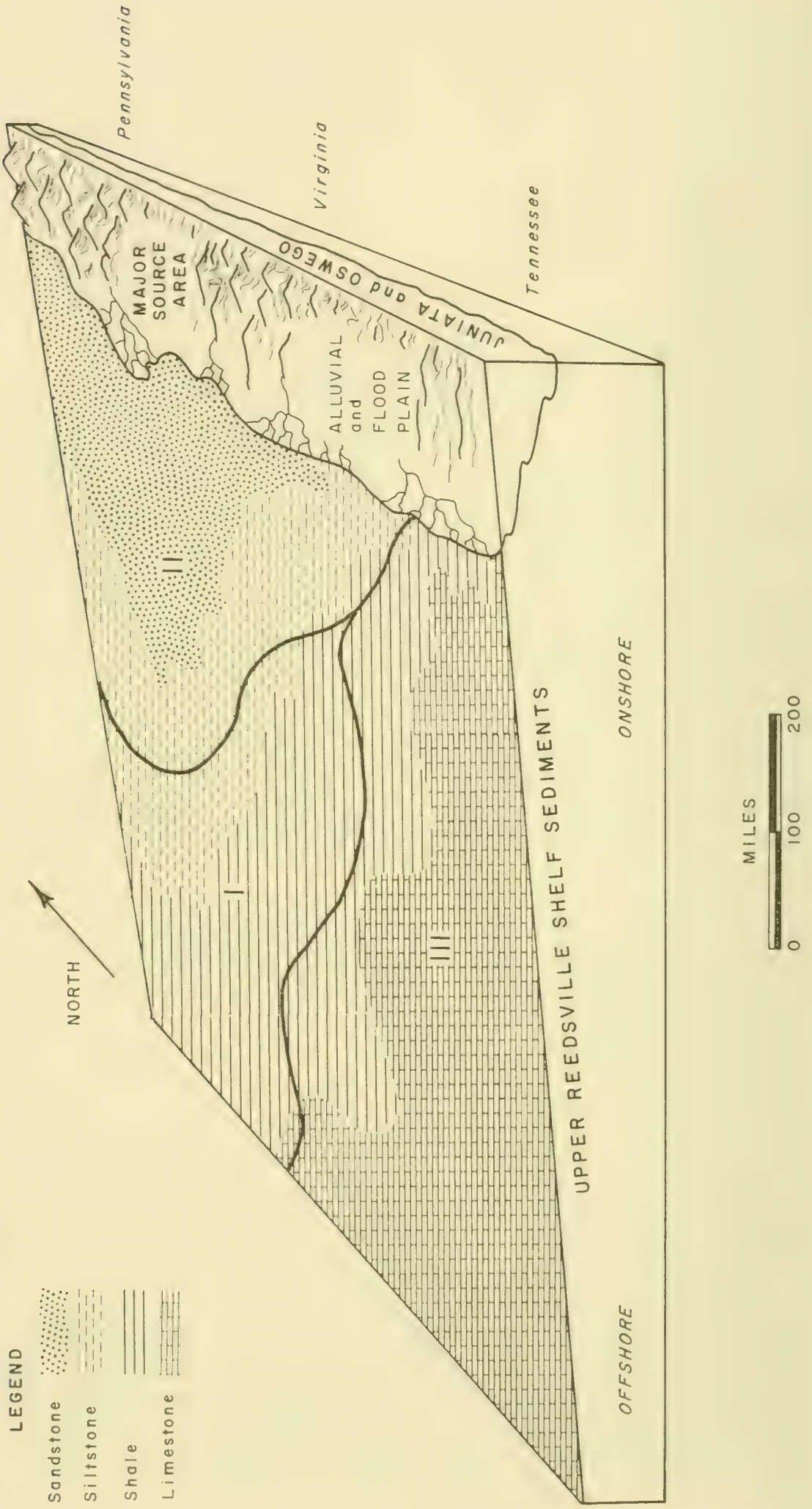
FIG. 24. Distribution of Late Ordovician faunal associations (Communities) in the central Appalachians. The data from Figures 13, 14, 16 and 17 are combined to form this distributional pattern (see Table 9 for species composition). Figure 6 outlines the stratigraphic relationships of the faunal association overlaps.

The communities are:

1. *Sowerbyella–Onniella* Community
2. *Orthorhynchula–Ambonychia* Community
3. *Zygospira–Hebertella* Community

Recent environments, an area of low primary benthonic productivity and poor circulation with a low level of oxidation, which is expressed in the texture and coloration of the sediments. The areas of high fossil diversities (A and A′ in Fig. 28) indicate regions of high primary productivity, normal marine bottom salinities, hence adequate circulation, and suitable substratum attachment sites for the numerous benthic, epifaunal suspension feeding trepostomatous bryozoans (A′) and the articulate brachiopods (A and A′). Also included in the high diversity in the north (A) are high numbers of infaunal deposit-feeding protobranch bivalve molluscs, which emphasize not only an adequate food supply for the suspension feeders but sufficient organic detritus to support a major infaunal element.

ENVIRONMENTAL SETTING—LATE ORDOVICIAN COMMUNITIES



SOWERBYELLA–ONNIELLA COMMUNITY

The fauna of the *Sowerbyella–Onniella* Community occupies an area extending from eastern and central Pennsylvania to north-central Virginia (see also Bretsky et al., 1969). The environmental setting was presumably outer sublittoral, slightly off and to the north of the Late Ordovician deltaic complex (see Figs. 25 and 26). The predominant substratum type was a silty mud and silt; the fauna appears to have been totally normal marine. Of the two populations which compose the *Sowerbyella–Onniella* Community, the Orthid–Crinoid Population is found most in silty muds, is dominated by *Onniella multisecta* and crinoids, and has an overall high faunal diversity (Table 10). This population grades seaward into a sparse trilobite fauna which is found in a dark lower Reedsville mud. Species in the Orthid–Crinoid Population grade shoreward into the Strophomenid Population. This latter population is completely dominated by the strophomenid brachiopods *Sowerbyella* (*Sowerbyella*) *sericea* and *Rafinesquina* "*alternata*". This Strophomenid Population is, however, only locally abundant in a medium to coarse silt and has a considerably lower faunal diversity than the Orthid–Crinoid Population (Table 10). The strophomenid brachiopods are gradually outnumbered by pleurotomariid gastropods in northern Virginia. Although more characteristic of coarser sediment than the Orthid–Crinoid Population, the Strophomenid population ends abruptly shoreward, showing little gradation into the faunas of the *Orthorhynchula–Ambonychia* Community, which occupies a similar type of bottom but closer to shore.

The faunas of both these populations tend to be patchily distributed within the *Sowerbyella–Onniella* Community and individuals of a species are often gregarious. The common epifaunal suspension feeders (articulate brachiopods) and epifaunal and infaunal detritus feeders (pleurotomariids and nuculoids) are rarely found mixed together, but recur throughout many local stratigraphic sections. The community is rather abruptly terminated in east-central Virginia, where it ends in a sequence of well-laminated silts and muds, totally unfossiliferous and seemingly undisturbed by biogenic activity. This environmental situation finds a Recent analogue in the deeper-water basin and sill environment described off the coast of southern California by Emery and Hulsemann (1962). Bayer (1967) outlined what appears to be an iso-community or parallel community from the Mid-Continent Upper Ordovician rocks. Bayer's *Thaerodonta* (= *Eoplectodonta*)*–Onniella* Community has as its major faunal components the *Sowerbyella*-like *Thaerodonta*, *Onniella*, *Ctenodonta similis* (a nuculoid, probably *Palaeoconcha*) and *Isotelus*.

FIG. 25. Environmental reconstruction of the Late Ordovician Communities in the central Appalachians based on stratigraphic, sedimentological and faunal evidence (see Fig. 24 which outlines the distribution of Upper Ordovician faunal associations directly from locality data with no environmental interpretations). The generalized distribution of the communities is portrayed at some time during the deposition of the Oswego barrier-lagoonal deposits along the northeastern shoreline. The communities are:

I. *Sowerbyella–Onniella* Community
II. *Orthorhynchula–Ambonychia* Community
III. *Zygospira–Hebertella* Community

The scale refers to distance along shoreline; onshore to offshore exaggeration is approximately ×4.

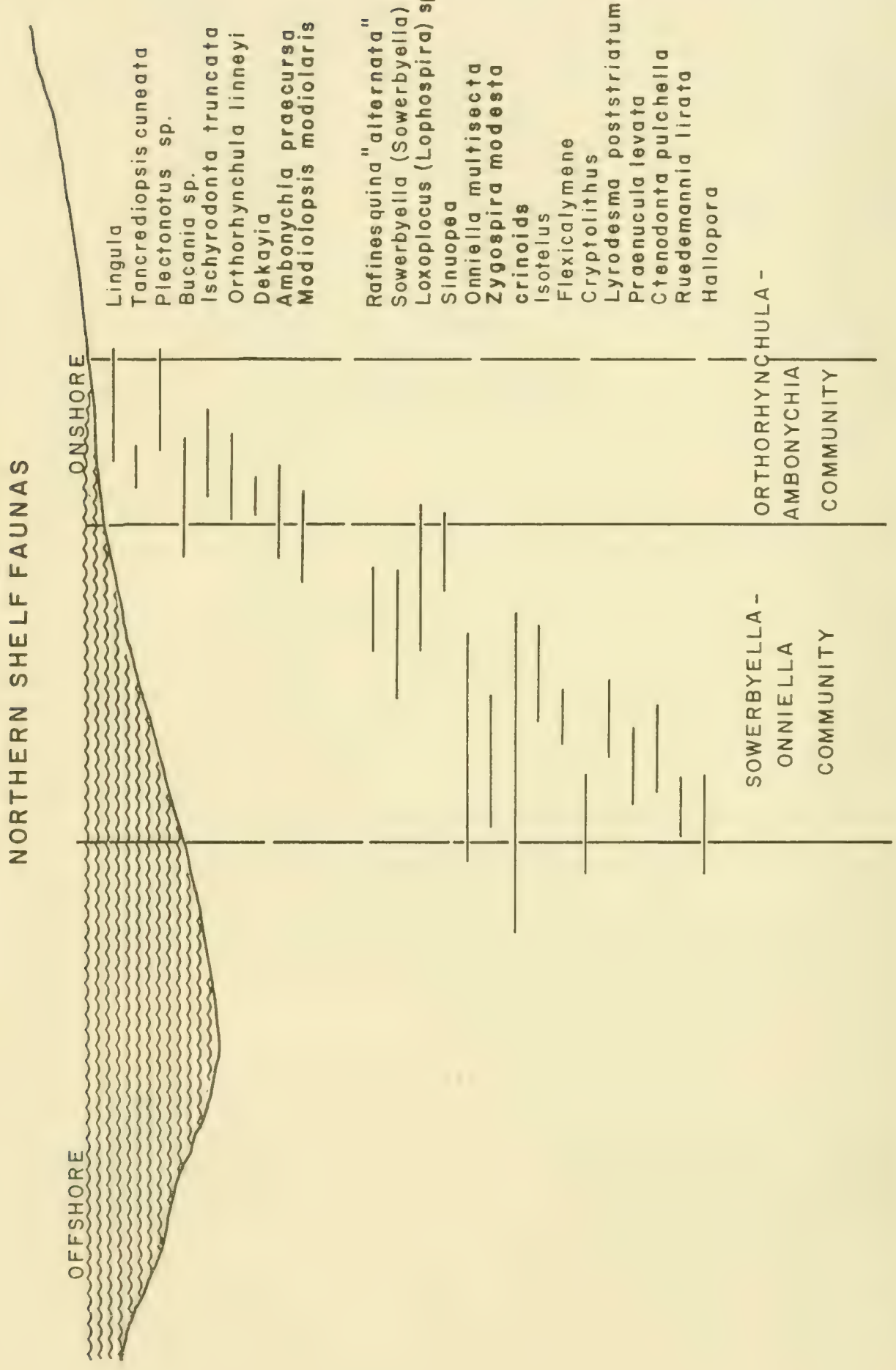


FIG. 26. The inferred distribution of the abundant faunas in the *Orthorhynchula–Ambonychia* and *Sowerbyella–Onniella* Communities. Refer to Figures 10, 11 and 12 for a more complete reconstruction of the sedimentological setting (cf. Fig. 27, southern shelf faunas).

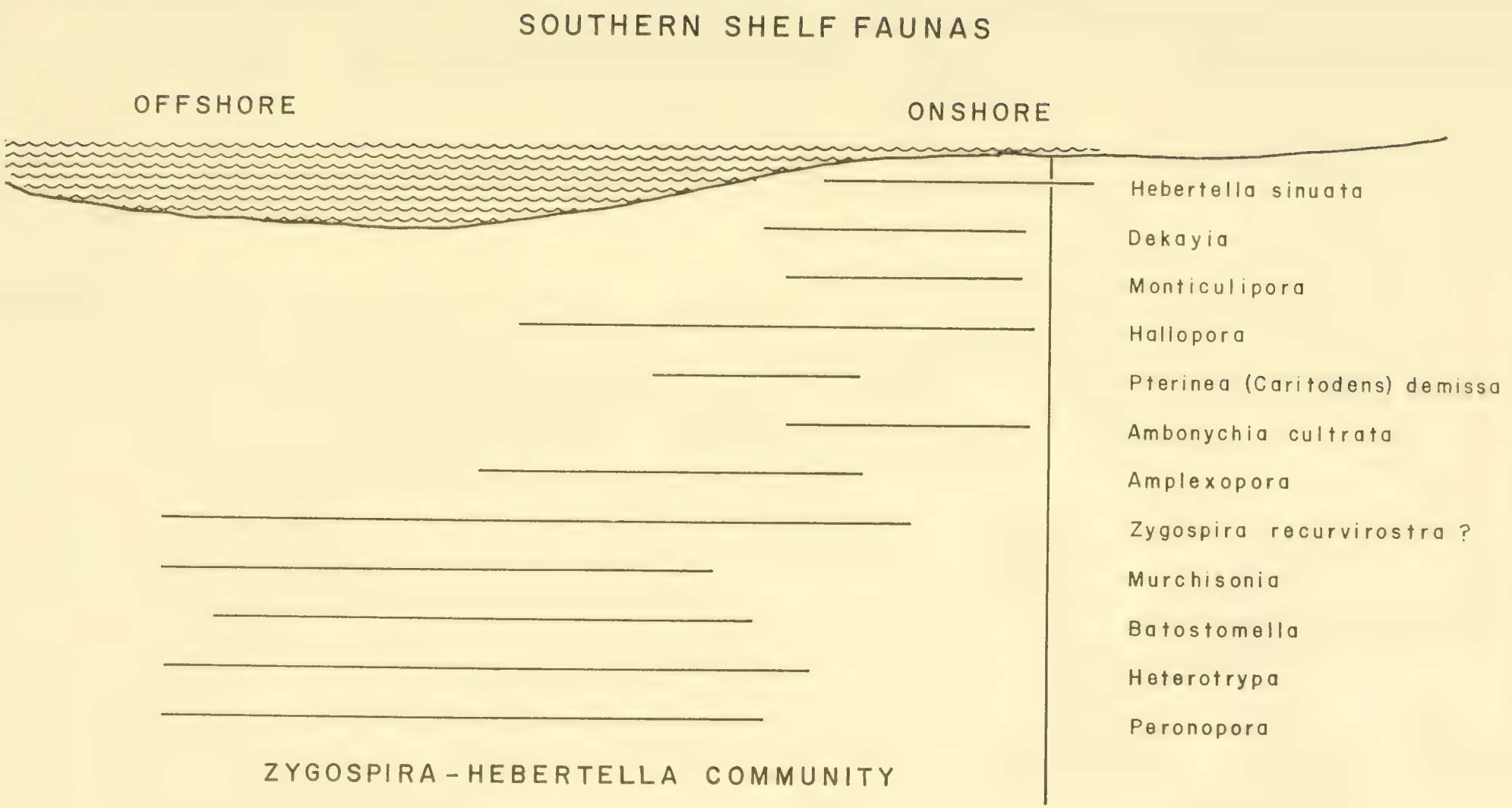
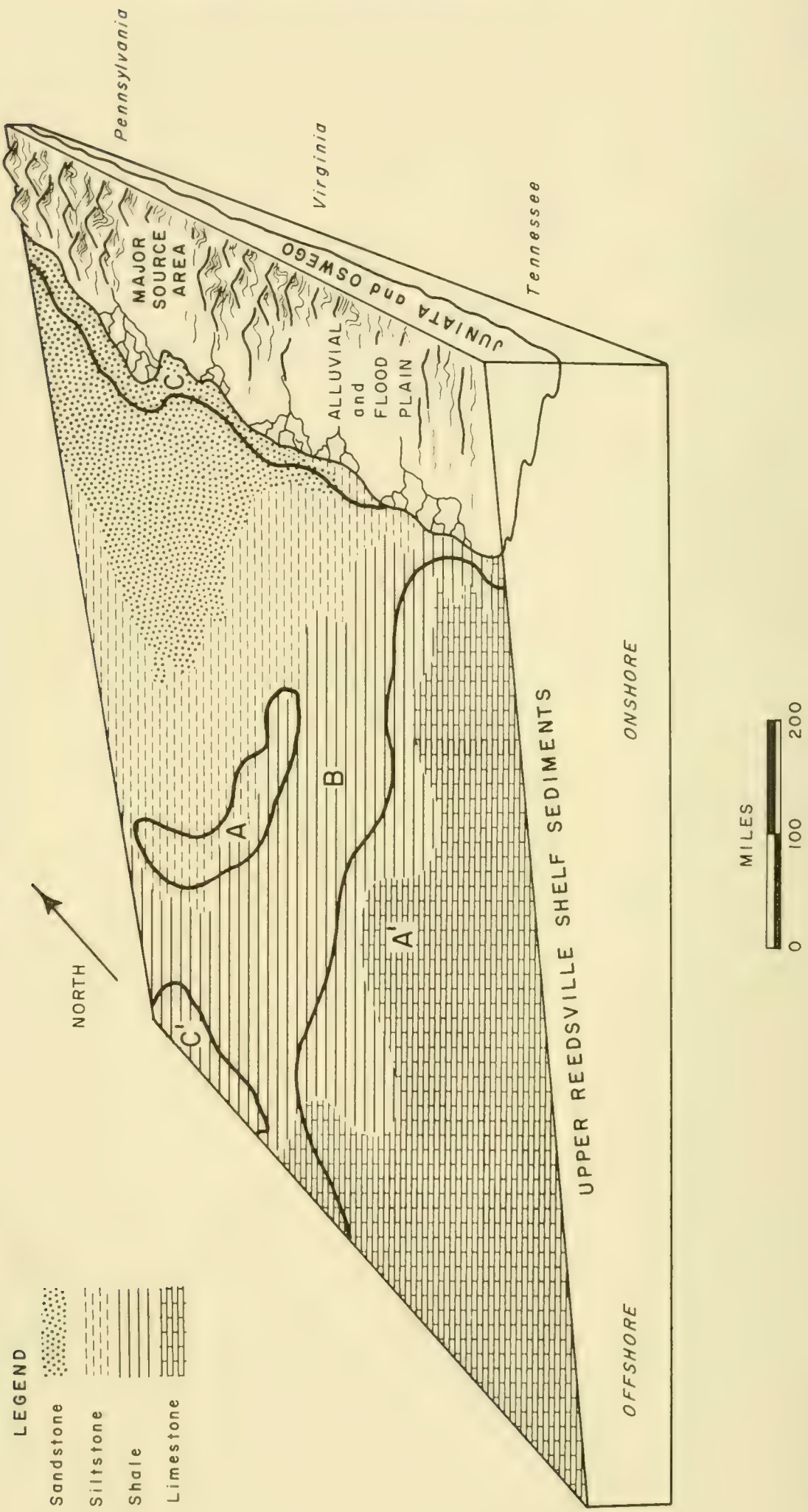


FIG. 27. The inferred distribution of the abundant faunas in the *Zygospira–Hebertella* Community. Refer to Figures 10, 11 and 12 for a more complete reconstruction of the sedimentological setting (cf. Fig. 26. northern shelf faunas).


LATE ORDOVICIAN DIVERSITY
Pennsylvania
Virginia
Tennessee
MAJOR SOURCE AREA
JUNIATA and OSWEGO
ALLUVIAL and FLOOD PLAIN
NORTH
A
B
C
A'
C'
UPPER REEDSVILLE SHELF SEDIMENTS
ONSHORE
OFFSHORE
MILES
0
100
200
LEGEND
Sandstone
Siltstone
Shale
Limestone

The Orthid–Crinoid Population may be compared to the Recent *Yoldia hyperborea* Community of Sparck (1937). This community is common in subarctic waters of 10 to 70 meters depth, and its fauna is dominated by a variety of infaunal, detritus feeding protobranchs (*Yoldia*, *Nucula* and *Leda*) in a muddy substratum. The Late Ordovician Orthid–Crinoid Population in north-central Pennsylvania consists, in part, of an abundant but patchy distribution of the infaunal photobranch genera *Ctenodonta*?, *Praenucula* and *Palaeoconcha*, also in a muddy substratum. The analogy is made to emphasize only an apparent similarity in the feeding habits of the abundant bivalve molluscs in Recent and Late Ordovician muds. Any extrapolation of depth and temperature conditions is very speculative.

ORTHORHYNCHULA–AMBONYCHIA COMMUNITY

The fauna of the *Orthorhynchula–Ambonychia* Community extends from south-central Pennsylvania to south-central Virginia. The environmental setting appears to have been predominantly inner sublittoral and intertidal. The sediments preserve a record of nearshore environments, including barriers, beaches and lagoons, and these particular faunas appear to have thrived only in this sedimentological regime (Figs. 25 and 26). The substratum was highly variable, from a muddy silt and silty sand to a coarse, well-sorted sand. It appears that members of the community were able to tolerate periods of variable salinity.

The nearest-shore fauna, the Linguloid Population, is dominated by large numbers of very few species (Table 10). This population is in some way related to the proximity of an upper Reedsville—lower Oswego shallow marine-barrier-lagoonal environment (see Fig. 8) that developed immediately south of the Late Ordovician deltaic complex in central Pennsylvania (Fig. 25). It is possible that the southward transport of sands by longshore currents from this deltaic complex permitted the development of the barriers. Directly seaward of the barriers in the upper Reedsville are found organically rich muddy silts and sands, highly reworked biogenically, and inhabited by a few eurytypic species able to tolerate the variable stress conditions such as changes in salinity and current reworking of the bottom sediment. Conditions of variable intensity of current reworking are manifested by occasional concentrated patches of phosphate grains, which accumulated in shallows during periods of low sedimentation, limited circulation and high productivity. In direct contrast are the interbedded,

FIG. 28. Reconstruction of Late Ordovician generic diversity in the central Appalachians based on apparent diversity as shown only by those animals preservable as fossils. It is important to note, however, that the onshore to offshore low fossil diversities are characteristic of Recent shelf environments. The stratigraphic-sedimentological framework is the one used in Figures 20-23 and Figure 25 (see esp. Fig. 25 for generalized environmental distribution of Late Ordovician communities).

Diversity	Genera
A & A′ — High	>15
B — Moderate	6-15
C & C′ — Low	1-5

The scale refers to distance along the shore; onshore to offshore exaggeration is approximately ×4.

TABLE 10. Central Appalachian Late Ordovician Communities and Populations.

1. *Sowerbyella–Onniella* Community	2. *Orthorhynchula–Ambonychia* Community	3. *Zygospira–Hebertella* Community
STROPHOMENID POPULATION	**LINGULOID POPULATION**	**SPIRIFERID POPULATION**
Brachiopoda: (strophomenids)	Brachiopoda: (linguloid)	Bryozoa: (trepostomes)
Sowerbyella (*Sowerbyella*) *sericea*	*Lingula*?	*Batostomella*
Rafinesquina "alternata"	(bellerophontids)	*Heterotrypa*
Gastropoda: (pleurotomariids)	Gastropoda: *Plectonotus*?	*Peronopora*?
Loxoplocus (*Lophospira*) *abbreviata*	*Bucania*?	*Monticulipora*
L. (*L.*) *perangulata*	Bivalvia: (nuculoid)	*Hallopora*
L. (*L.*) *ventricosta*	*Tancrediopsis cuneata*	*Amplexopora*
Sinuopea?	(modiomorphid or trigonoid)	Brachiopoda: (spiriferid)
ORTHID–CRINOID POPULATION	*Ischyrodonta truncata*	*Zygospira recurvirostra*
Bryozoa: (trepostome)	**RHYNCHONELLID POPULATION**	Gastropoda: (murchisoniid)
Hallopora	Bryozoa: (trepostome)	*Murchisonia*?
Brachiopoda: (orthid)	*Dekayia*	Bivalvia: (pterioid)
Onniella multisecta	Brachiopoda: (rhynchonellid)	*Pterinea* (*Caritodens*) *demissa*
(spiriferid)	*Orthorhynchula linneyi*	(ambonychiids)
Zygospira modesta	Bivalvia: (modiomorphid)	*Ambonychia cultrata*
(strophomenid)	*Modiolopsis modiolaris*	*Ambonychia radiata*?
Sowerbyella (*Sowerbyella*) *sericea*	(ambonychiid)	(modiomorphid)
Gastropoda: (pleurotomariid)	*Ambonychia praecursa*	*Modiolopsis modiolaris*
Ruedemannia? *lirata*	**MODIOLOPSID POPULATION**	**ORTHID POPULATION**
Bivalvia: (nuculoids)	Bivalvia: (modiomorphid)	Bryozoa: (trepostomes)
Ctenodonta? *pulchella*	*Modiolopsis modiolaris*	*Hallopora*
Praenucula levata	(ambonychiids)	*Dekayia*
Lyrodesma poststriatum	*Ambonychia praecursa*	*Monticulipora*
(ambonychiid)	*Ambonychia cultrata*	Brachiopoda: (orthid)
Ambonychia radiata		*Hebertella sinuata*
Trilobita: *Isotelus*		(rhynchonellid)
Flexicalymene		*Orthorhynchula linneyi*
Cryptolithus		(strophomenid)
Crinoidea: crinoid columnals — unidentifiable		*Rafinesquina "alternata"*

TABLE 11. A summary of the central Appalachian Upper Ordovician Communities. Included is a brief outline of possible Recent analogues which must be viewed, however, as only very general approximations. The material incorporated within this table is reviewed in the text.

Communities	*Sowerbyella–Onniella*	*Orthorhynchula–Ambonychia*	*Zygospira–Hebertella*
Geographic location	eastern and central Pa. to north-central Va.	south-central Pa. to south-central Va.	southwestern Va. and northern Tenn.
Major substratum type	silts — silty muds	sands — muddy silts	silty muds — muds — lime muds
Inferred environmental setting	outer sublittoral; seaward of deltaic complex.	shallow inner sublittoral and intertidal, including barrier–beach–lagoonal environments; integrally associated with deltaic complex sedimentation.	inner and outer sublittoral on a broad, gently sloping shelf; south of main deltaic complex and influx of terrigenous clastics; possible tidal flat environments.
Possible recent analogues to Late Ordovician populations	Orthid–Crinoid Population: *Yoldia hyperborea* Community, muds — 10 to 70 meters — subarctic — abundant *Yoldia, Nucula, Leda* (Sparck, 1937).	Linguloid Population: 1. Enclosed lagoon — North Gulf (Parker, 1960). 2. *Nucula proxima-Nepthys incisa* Community, muds, silty muds — L. I. Sound, Buzzards Bay (Sanders, 1953, 1956, 1960). 3. *Syndosmya* Communities, shallow mud bottoms, sheltered and estuarine Danish waters (Thorson, 1957).	Spiriferid Population: *Turritella* or *Cerithium* Communities, soft mud bottoms, shallow to moderate inner sublittoral depths (Thorson, 1957).

well-sorted, cross-bedded sands of the bars and barriers. Figure 29 reconstructs a very general environmental setting of the Linguloid Population, showing both the dominance of the epifaunal and infaunal detritus feeders and the probable primary food source in the lagoonal and off-beach algal stands. The beach and tidal flat environments of the lower Oswego are characterized by only a few elongate, slender, vertical worm tubes and a very few linguloids. Seaward, however, the Linguloid Population grades rapidly into the Rhynchonellid and Modiolopsid Populations. The former, dominated by *Orthorhynchula linneyi* and *Ischyrodonta truncata*, is located seaward of the bars and barriers where there is a sandy bottom, whereas the Modiolopsid Population, *Ambonychia praecursa* and *Modiolopsis modiolaris*, seems to have preferred a muddier substratum. Gradations are common between these two latter populations, but where the silts become extremely muddy only the Modiolopsid Population, and *Modiolopsis modiolaris* in particular, is numerous. The faunas of both Rhynchonellid and the Modiolopsid Populations are composed of epifaunal suspension feeders, of moderate diversity, occasionally patchy in distribution, resembling Recent shallow mussel-dominated habitats. The sediment is, however, often thoroughly reworked; a major infaunal element may thus have been locally present. Whereas the Linguloid Population ends abruptly in central Virginia (see Fig. 6) with little evidence of mixing with the *Zygospira–Hebertella* Community, some species of the Rhynchonellid and Modiolopsid Populations grade over a fairly broad area with the dominant southern faunas. In the north there is only a very limited seaward mixing with the faunas of the *Sowerbyella–Onniella* Community.

A review of the Recent marine literature points up three possible modern analogues to the Linguloid Population: the enclosed lagoonal assemblage along the northern coast of the Gulf of Mexico (Parker, 1960, p. 310); the *Nucula proxima–Nepthys incisa* Community in the muds of Buzzards Bay, Massachusetts, and Long Island Sound (Sanders, 1956, 1958, 1960); and the *Syndosmya* Communities in the sheltered mud bottoms and estuaries along the coast of Denmark (Thorson, 1957, p. 510). In diversity, numbers and kinds of species, bathymetric position and substratum type, these Recent communities are quite comparable to the Late Ordovician environmental setting of the Linguloid Population.

ZYGOSPIRA–HEBERTELLA COMMUNITY

The fauna of the *Zygospira–Hebertella* Community extends over much of southwestern Virginia and northern Tennessee. The environmental setting appears to have included both inner and outer sublittoral regimes, with possibly an occasional lagoonal or tidal flat occurrence. The broad, gently sloping shelf that seems to have existed in the south-central Appalachians during the Late Ordovician allowed for the development of a virtual shallow epicontinental sea. This area was well south of the major terrigenous influx (Figs. 25 and 27). The predominant substratum type was a silty mud, mud and lime mud. The environment appears to have been normal marine in character with the exception of a few places where brackish water would have existed on low, gently sloping tidal flats.

In the central Appalachians the *Zygospira–Hebertella* Community is the closest approximation to a typical, highly diversified Mid-Continental shallow sea fauna.

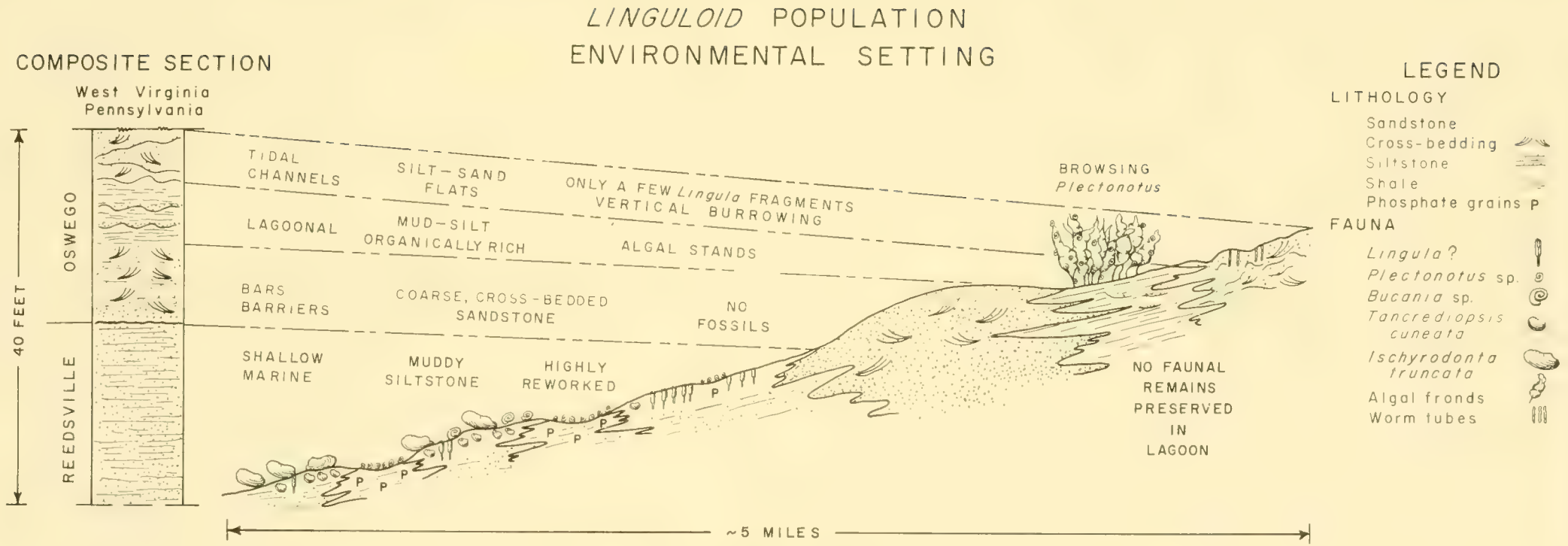

LINGULOID POPULATION
ENVIRONMENTAL SETTING
COMPOSITE SECTION
West Virginia
Pennsylvania
40 FEET
OSWEGO
REEDSVILLE
TIDAL CHANNELS
SILT–SAND FLATS
ONLY A FEW *Lingula* FRAGMENTS
VERTICAL BURROWING
BROWSING
Plectonotus
LAGOONAL
MUD–SILT
ORGANICALLY RICH
ALGAL STANDS
BARS
BARRIERS
COARSE, CROSS-BEDDED
SANDSTONE
NO
FOSSILS
SHALLOW
MARINE
MUDDY
SILTSTONE
HIGHLY
REWORKED
NO FAUNAL
REMAINS
PRESERVED
IN
LAGOON
~5 MILES
LEGEND
LITHOLOGY
Sandstone
Cross-bedding
Siltstone
Shale
Phosphate grains P
FAUNA
Lingula?
Plectonotus sp.
Bucania sp.
Tancrediopsis cuneata
Ischyrodonta truncata
Algal fronds
Worm tubes

FIGURE 29.

The community is dominated by epifaunal suspension feeders. The species are generally very widespread and the individual populations tend to be much less patchy than those in the north-central Appalachians. Although both Spiriferid and Orthid Populations contain numerous trepostomatous bryozoans, *Zygospira recurvirostra* is consistently characteristic of the muds and lime muds, along with a variety of epifaunal, suspension feeding ambonychiid and pterioid bivalves and the possibly epifaunal murchisoniid gastropods. The Orthid Population is characterized by numerous *Hebertella sinuata* and the trepostomes *Monticulipora* and *Dekayia* in silty muds and muddy silts. The Spiriferid and Orthid Populations intergrade over the entire area covered by the *Zygospira–Hebertella* Community, and both also exhibit considerable mixing with the Rynchonellid and Modiolopsid Populations of the *Orthorhynchula–Ambonychia* Community to the north and northeast. There is, however, only limited mixing with the deeper-water *Sowerbyella–Onniella* Community to the north.

There is one possible Recent analogue to the Spiriferid Population, the *Turritella* or *Cerithium* Communities that occupy soft mud bottoms at shallow to moderate inner sublittoral depths (Thorson, 1957, p. 514). The analogy is again only a rough approximation of the probable Late Ordovician environmental settings. Table 11 is a brief survey of the environmental settings and probable Recent analogues of the central Appalachian Late Ordovician communities.

CONCLUSIONS

This study has shown that the Upper Ordovician rocks in the central Appalachians enclose a shallow marine fauna that exhibits not only a distinctive onshore to offshore distributional pattern but also a longshore one. The combined zoogeographic and autecological study also has pointed out that the nearshore environments are commonly dominated by bellerophontid gastropods, nuculoid and modiomorphid bivalve molluscs, and linguloid and rhynchonellid brachiopods, whereas the offshore regimes are composed predominantly of orthid, strophomenid and spiriferid brachiopods, crinoids and trepostomatous bryozoans. This general distributional pattern is modified significantly by the position of the major source area in central Pennsylvania as the characteristically offshore brachiopods and bryozoans come to occupy more nearshore environments in southwestern Virginia and northern Tennessee farther away from this major deltaic complex. The effect of this deltaic complex acting as a barrier to the migration and dispersal of the Late Ordovician benthic marine invertebrates has yet to be explored in detail since this study was confined exclusively to those marine environments immediately off and to the south of the complex.

The recognition of these three Late Ordovician benthic invertebrate communities furthermore has emphasized the likelihood of mapping parallel benthic communities for any segment of the geologic past, and will not only permit more detailed explanations of the evolutionary development of selected taxonomic groups, but also presents the issue of community stability and evolution over extended periods of geologic time. Many problems of the evolution of stable community structures — what kinds of benthic communities are stable, where they are most stable and how long they remained stable — remain virtually untouched. Additional studies of Late Ordovician fossiliferous rocks in eastern and central North America should provide the data needed to elaborate the development of benthic community structures on these Late Ordovician shelf environments. Only a few other Paleozoic studies, however, have emphasized the community approach in studying the history of life. The most noteworthy contributions are Copper's (1966) study of Devonian atrypid brachiopods, which is primarily autecological; and the synecological studies of Elias (1937), Johnson (1962), Zangerl and Richardson (1963), Laporte (1967), Stevens (1966) and Sutton et al. (1966). There is a great need for further detailed paleoecological investigations throughout the entire Paleozoic record in order to attempt to trace well-defined fossil communities throughout this extended period of geologic time.

Although the structure of marine benthic communities is generally thought to be relatively uncomplicated, and the basic food-web pattern (producers, consumers, decomposers and transformers) was probably established by the early Paleozoic, the prospects for studying community evolution in the Paleozoic are especially promising. This is the time of initial phylogenetic radiation of many invertebrate groups. The

length of time a community maintains a constant faunal composition would seem to provide a key to the evolution of a stable community structure. By tracing the evolution of marine invertebrate community structures throughout a long period of geologic time, we can begin to document variable rates of change in the faunal composition of the community and thus recognize particular benthic environmental settings where community stability or instability exists.

A synthesis of detailed Paleozoic community faunal compositions should point out major changes in the faunal composition on benthic communities at particular times and in specific places on the marine shelf. Periods of major reorganization of shelf invertebrate faunas are well known and have been the subject of numerous papers especially concerned with the causal factors in this change in faunal composition. To date one of the more serious flaws in any discussion of the paleoecology and evolution of benthic invertebrates is that the invertebrate taxa have been considered as almost exclusively separate entities or as parts of only a very general marine realm. With increased knowledge of these ancient communities, species and higher categories may be viewed as part of an integrated community structure subject to a variety of biotic and physio-chemical factors whose interactions determine the stability or instability of the organization of a particular community.

SYSTEMATIC PALEONTOLOGY

INTRODUCTION

In this study of the central Appalachian Upper Ordovician faunas more than 95 per cent of the total fauna belonged to three phyla: Bryozoa, Brachiopoda and Mollusca (Gastropoda and Bivalvia). Specimens of Arthropoda (Trilobita) and Echinodermata (Crinoidea) were much more scattered and rare. Since identification of the abundant specimens was critical to the outlining of the zoogeographic distribution and faunal associations, preliminary ecological data, identifications, and descriptions of the various Bryozoa, Brachiopoda, Gastropoda and Bivalvia were submitted to specialists within each field for their critical evaluation. Species-level taxonomy was normally possible within the Brachiopoda and Mollusca, given sufficiently well-preserved materials. Within the Bryozoa, however, generic identifications were thought reasonably sound, but species-level taxonomy in this group awaits a more thorough taxonomic investigation.

For the major part of this study, I examined material which I had collected from the central Appalachians. Descriptions and identifications, however, were reviewed in light of the relevant comparative literature for the Paleozoic of North America as well as some outstanding taxonomic contributions on the Lower Paleozoic faunas of Europe. I attempted to place each central Appalachian taxon into the most acceptable category. No new taxa are introduced, but my reservations concerning any particular classification are placed in the discussion of each taxon. Synonymies are included where species-level identification seemed feasible in view of the data I had accumulated. Previous descriptions from strictly systematic literature could, I believe, be somewhat more critically evaluated in light of the new ecological data, i.e., an integrated morphological and distributional approach. It cannot be overstressed that features unknown to me in any of the taxa described may be found in other collections. The following descriptions pertain only to those specimens collected by me from the Upper Ordovician rocks of the central Appalachians.

The format used in this section normally consists of Synonymy-Description-Materials-Discussion for each species, but a general discussion is substituted where species-level taxonomy was not possible. All the materials used in this study are deposited in the Peabody Museum of Yale University along with a complete card index indicating species abundance, faunal and lithologic associations for the individual taxon at each locality and/or horizon. Localities are listed by number on p. 135.

BRYOZOA

Plates 3-9

The Bryozoa constitute an important faunal element in the central Appalachian Upper Ordovician clastic facies. Although normally less abaundant than the Mollusca and Brachiopoda, Bryozoa may be co-dominant locally with spiriferid, orthid and rhynchonellid brachiopods.

A survey of the central Appalachian Ordovician literature reveals an almost complete lack of recent bryozoan taxonomic investigations, and as Boardman and Utgaard (1966, p. 1082) pointed out, there are few usable illustrations of the established Paleozoic taxa. Current taxonomic philosophies and concepts stress the re-evaluation of type materials through extensive microsectioning; much of the pre-1960 bryozoan literature lacks adequate treatment of microstructure and therefore is of limited use. Utgaard and Perry (1964) presented detailed descriptions of some Upper Ordovician trepostomatous bryozoans and included a valuable historical review of these changing taxonomic philosophies with special reference to the Cincinnatian Mid-Continent species. Recent papers of taxonomic value used in studying the Bryozoa are those of Bassler (1953), Boardman (1960), Ross (1963) and Brown (1965). Particularly useful were earlier papers by Cumings (1908) and Cumings and Galloway (1913, 1915), in which numbers of zooecial wall microstructures were examined in detail for the first time.

The current taxonomic re-evaluation by those investigators mentioned above places the definition of many Paleozoic taxa in doubt. I have undertaken only a generic-level assignment of the central Appalachian bryozoan taxa. Species-level bryozoan taxonomy would not have contributed materially to this study and probably should await complete taxonomic reviews.

Phylum BRYOZOA
Subphylum ECTOPROCTA
Class GYMNOLAEMATA
Order TREPOSTOMATA
Suborder AMALGAMATA
Family MONTICULIPORIDAE

Genus *MONTICULIPORA*

Plate 3, figures 1-3

Identification of the genus *Monticulipora* is based on the analysis of 12 microsections of specimens from localities in southwestern Virginia. The zoaria are characteristically ramose and frondescent; the median diameter of the 12 sectioned specimens is 11 mm. Zooecial walls are thin in the endozone but finely laminated zooecial linings are present in the exozone. Planar and cystose diaphragms are abundant throughout the entire zooecium. Mesopores are common and clustered on monticules; there are few acanthopores and these occur only at zooecial corners.

Assignment of these specimens to the genus *Monticulipora* is substantiated by the recent generic redescription by Boardman and Utgaard (1966, p. 1093). Excellent plates and descriptions of certain Cincinnatian species of *Monticulipora* are also pre-

sented by Utgaard and Perry (1964, p. 42). I tried to avoid possible misidentification of these specimens with the very similar genera *Prasopora* or *Prasoporina* by using an extensive Paleozoic trepostome catalogue made available to me by Dr. Richard Boardman of the U. S. National Museum.

The genus *Monticulipora* is abundant (see Table 3 for numbers; relative density index equal to or greater than 3) only at localities 141 and 142 in southwestern Virginia, although it is present at a number of nearby localities (loc. 132, 128, 125; possibly 126 and 140; see Fig. 1). Where *Monticulipora* is abundant, the most commonly associated faunal elements are a smaller ramose *Dekayia*, *Zygospira recurvirostra*, *Ambonychia cultrata*, *Pterinea* (*Caritodens*) *demissa*, and *Modiolopsis modiolaris*, all part of the Spiriferid Population of the *Zygospira–Hebertella* Community. *Monticulipora* is geographically confined to southwestern Virginia and northern Tennessee; its distribution is much like that of *Batostomella* and *Amplexopora*, i.e., bryozoan faunal province III (see Fig. 13). The associated faunal elements, including *Dekayia*, are more widely distributed geographically than is *Monticulipora*.

Family HETEROTRYPIDAE

Genus *DEKAYIA*

Plate 3, figure 4; plate 4, figures 1-6; plate 5, figures 1-4

Identification of the genus *Dekayia* is based on the analysis of 41 microsections of specimens from localities in West Virginia, Virginia, and Tennessee. The zoaria are commonly ramose and have a median diameter of 9 mm. Only a few encrusting forms have been identified. Zooecial walls are characteristically thin and crenulated in the endozone, but there are distally curved, finely laminated zooecial linings in the exozone. There are a few thin, simple diaphragms in each zooecium; they are irregularly spaced in the exozone. Mesopores are rare, but acanthopores are common and are usually exozonal, oblique to the axis of the zooecia and occur at the zooecial corners.

The genera *Dekayia* and *Dekayella* were cited by various investigators as occurring in the central Appalachian Upper Ordovician clastic facies, but their figures and descriptions, for the most part, depended on hand specimens and are now of little use. It was not until Boardman and Utgaard (1966, p. 1103) emended the definitions of *Dekayia* and *Dekayella* that I was able to assign these Upper Ordovician specimens to the genus *Dekayia*. *Dekayella* is considered by them to be a junior subjective synonym of *Heterotrypa*.

Dekayia is one of the most widespread Bryozoa in the Upper Ordovician clastic facies (bryozoan faunal provinces II and III, see Fig. 13); only *Hallopora* is more widely dispersed. *Dekayia* is numerous in three distinctive faunal associations, the Spiriferid and Orthid Populations of the *Zygospira–Hebertella* Community and the Rhynchonellid Population of the *Orthorhynchula–Ambonychia* Community. Table 12 outlines these associations.

West Virginia locality 203 exhibits a particularly well-exposed section where there is a change in the external morphology of *Dekayia* specimens accompanying a change in the silt-mud ratio. Figure 30 depicts about 40 feet of this upper Reedsville section at locality 203 (North Fork Mountain, West Virginia). At least two samples (A-6301, A-6302) contain abundant fine, stem-like fragments in a silty mudstone. Fifteen to

TABLE 12. The associated faunal elements of *Dekayia* in northern Tennessee, southwestern Virginia and eastern West Virginia.

	Cumberland Mt., Va. Big Ridge and Wallen Ridge, Tenn.	Powell Mt., Va.	East River Mt., Peters Mt., Va. North Fork Mt., Va. and W. Va.
Locality numbers	128,132,137	141	186,190,202,203
Associated faunal elements	*Hallopora* *Hebertella sinuata* *Zygospira recurvirostra* *Murchisonia?*	*Monticulipora* *Zygospira recurvirostra* *Ambonychia cultrata* *Modiolopsis modiolaris* *Pterinea (Caritodens) demissa*	*Orthorhynchula linneyi* *Modiolopsis modiolaris* *Ambonychia praecursa*
Population	Orthid	Spiriferid	Rhynchonellid
Substratum	mud and silty mud	silty mud	muddy silt and silt

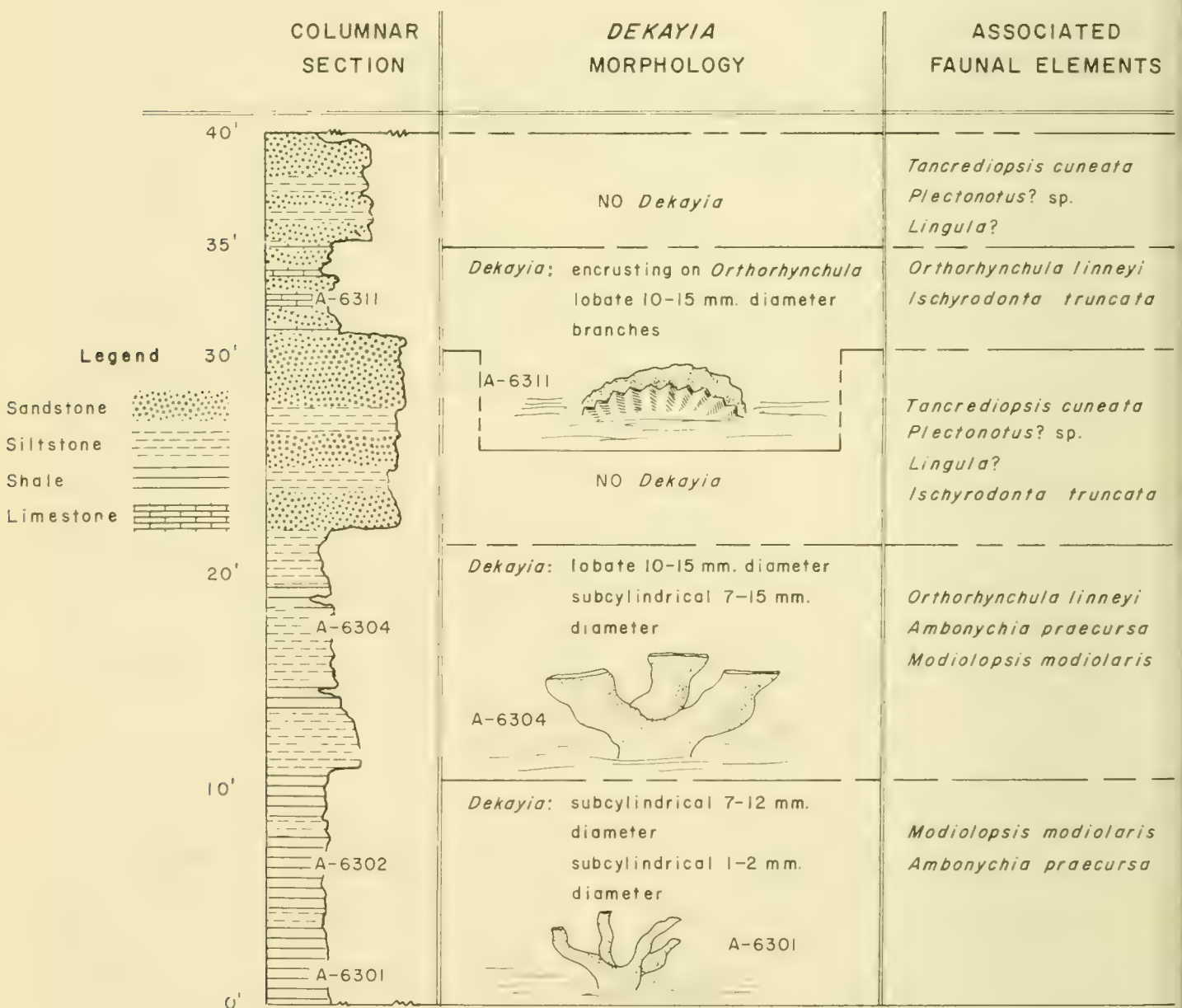


FIG. 30. Variability in external morphology of the trepostome genus *Dekayia* at locality 203 North Fork Mountain, West Virginia. "A-numbers" refer to the Peabody Museum catalogued collection.

twenty feet above the bed containing these two samples, sample A-6304 contains abundant larger cylindrical branches in addition to a few massive lobate forms in a muddy siltstone. The final appearance of numerous *Dekayia* specimens is in sample A-6311, where massive lobate and encrusting forms predominate in a shelly siltstone. The encrusting *Dekayia* are usually found on the disarticulated valves of the large rhynchonellid brachiopod *O. linneyi*. *Dekayia* is absent where the sands are fairly well sorted and there is sedimentological evidence of considerable substratum mobility, such as channeling and intraformational conglomerates.

These three distinct morphological types of Bryozoa in the Upper Ordovician are similar to modern (or Recent) bryozoan shapes and may serve as indicators of environmental setting. The nature of the substratum and the intensity of the water movement appear to be the main controlling factors in bryozoan morphology off the present Rhone delta (Lagaaij and Gautier, 1965). In the Upper Ordovician, the finer subcylindrical forms are more common in the muddier sediments; the stout lobate and encrusting habits predominate where there is a higher percentage of sand and silt (Fig. 30). All were presumably firmly attached to the substratum. Where *Dekayia* is abundant, the rates of deposition were apparently low to moderate, but turbulence may have been at a maximum higher in the section where the substratum consisted of sand and rhynchonellid brachiopod shells. All of these morphological habits are common in the Recent sublittoral, but the encrusting form may also occur in littoral regions where there is some protection from the rigors of a very turbulent environment.

Family BATOSTOMELLIDAE

Genus *BATOSTOMELLA*

Plate 6, figures 1-3

Identification of the genus *Batostomella* is based on the analysis of 45 microsections of specimens from southwestern Virginia and northern Tennessee. The zoaria are ramose and show a median diameter of 8 mm. The zooecial walls are thick and mural lacunae are occasionally abundant. Diaphragms are thin, planar and spaced regularly throughout the zooecium. Subangular mesopores are common but there are few acanthopores.

Assignment of these common Upper Ordovician specimens to the genus *Batostomella* was aided by the use of plates and descriptions given by Utgaard and Perry (1964, p. 85) and Bassler (1953, p. G99). Dr. Richard Boardman also made available an extensive catalogue of Paleozoic trepostome genera.

Specimens of *Batostomella* are abundant at localities 125, 126 and 140 in southwestern Virginia and northern Tennessee (see Table 3, Clinch Mountain), i.e. bryozoan faunal province III (see Fig. 13). As with many other trepostomes, fragments can be found at a number of nearby localities. Specimens from locality 126 are four to five times larger in diameter than those from localities 125 and 140. These larger, ramose stems average between 12 and 15 mm in diameter and show a slight increase in the number of mesopores and an abundance of mural lacunae. Finer, more delicate branches (2 to 3 mm in diameter) occur at localities 125 and 140; the zooecial walls show few, if any, mural lacunae. Boardman (pers. comm.) emphasized the importance of mural lacunae, pointing out that they have been found previously in abundance only in species of Richmond age (upper Upper Ordovician). Thus there

may be not only specific differences between the *Batostomella* specimens at locality 126 and those at localities 125 and 140, but also a slight temporal discrepancy. There is, however, no significant change in the associated faunal elements: *Hallopora, Zygospira recurvirostra* and *Modiolopsis modiolaris,* which are part of the Spiriferid Population of the *Zygospira–Hebertella* Community.

Localities 125 and 140 contain, in addition to *Batostomella,* about 20 fragments of *Heterotrypa* (Pl. 7, figs. 1-2) and a peronoporid trepostome (Pl. 6, figs. 4-6). The peronoporid appears to have been an encrusting form, rather than the more common frondose, bifoliate morphological type.

The characteristic grouping of trepostomatous Bryozoa (*Batostomella, Hallopora, Heterotrypa* and *Peronopora*?) in addition to *Zygospira recurvirostra* forms a part of the Spiriferid Population and is found only along the eastern margin (Clinch Mountain, see Fig. 7) of upper Reedsville exposures in southwestern Virginia and northern Tennessee. At locality 140, where muddy siltstones rather than calcareous mudstones begin to dominate the upper portions of the Reedsville section, numerous specimens of *Batostomella* are found about 30 to 40 feet below strata dominated by *Ambonychia cultrata, Ischyrodonta truncata, Modiolopsis modiolaris,* and some *Dekayia* and *Monticulipora,* also part of the Spiriferid Population. These latter trepostomes, commonly higher in the section, are larger ramose forms in a muddy silt, occasionally encrusting on one another, whereas *Batostomella* is confined to a calcareous mud, always finely ramose, never encrusting.

The Richmondian age of *Batostomella* and the possibility of a Richmond species of *Hallopora* in northern Tennessee (see below p. 75), in contrast to northern faunal elements that are definitely Maysvillian, points up the possibility of a slight decrease in the age of the faunal assemblage from the north-central to the south-central Appalachians. This would appear to coincide with the expected variations in rate of progradation from east to west throughout Late Ordovician time. It seems that the environments in the more northerly localities throughout the Late Ordovician would be less static and hence only Maysvillian forms have been preserved. The areas in the south, experiencing a considerably diminished and diluted terrigenous influx, would remain environmentally stable for a somewhat longer period of time, perhaps into the Richmondian.

Suborder INTEGRATA
Family AMPLEXOPORIDAE

Genus *AMPLEXOPORA*
Plate 7, figures 3-6; plate 8, figures 1-4

The identification of the genus *Amplexopora* is based upon analysis of seven microsections from southwestern Virginia. The zoaria are ramose and have a median diameter of 12 mm. Zooecial walls are thick and integrate in the exozone and have well-developed laminated zooecial linings. There are a few planar diaphragms regularly spaced within the exozone. Mesopores are absent and acanthopores few.

Assignment of these specimens to the genus *Amplexopora* was aided by the plates and descriptions given by Boardman (1960, p. 16) in his revision of the genus *Am-*

plexopora. Specimens were positively identified only at localities 131 and 138, whereas at locality 141 *Amplexopora* could be tentatively identified only from two specimens which came from an assemblage that had fewer trepostome zoaria, i.e. bryozoan faunal province III (see Fig. 13). *Amplexopora* is found at sites with numerous specimens of *Zygospira recurvirostra, Pterinea* (*Caritodens*) *demissa* and *Ambonychia cultrata*, somewhat less common *Hebertella sinuata*, and fragments of a peronoporid trepostome; all part of the Spiriferid Population of the *Zygospira–Hebertella* Community. The external morphology of *Amplexopora* is no different from that of the other abundant trepostomatous Bryozoa, emphasizing the existence of fairly uniform, quiet water conditions throughout much of the southwestern Virginia and northern Tennessee area during the Late Ordovician.

Family HALLOPORIDAE

Genus *HALLOPORA*

Plate 9, figures 1-6

Identification of the genus *Hallopora* is based on the analysis of 57 microsections of specimens from southwestern Virginia and northern Tennessee, and 11 microsections from central Pennsylvania. The zoaria are ramose and show a median diameter of 2 mm in southwestern Virginia and northern Tennessee, increasing to 10 mm in central Pennsylvania. Zooecial walls are thick and integrate in the exozone and have laminated zooecial linings. Thin, planar diaphragms are crowded near the exozone. Mesopores are abundant and clustered on monticules, whereas acanthopores are absent.

Hallopora is one of the most characteristic and distinctive Upper Ordovician trepostomes. The assignment of these central Appalachian specimens to this genus was made with the aid of plates and descriptions given by Bassler (1953, p. G112) and Utgaard and Perry (1964, p. 101).

Hallopora is abundant at localities in central Pennsylvania (loc. 34, 34A, 36) and southwestern Virginia-northern Tennessee (loc. 127, 137, 147, 184) and is the most widespread central Appalachian trepostome. *Hallopora* characterizes two quite geographically distinct bryozoan faunal provinces; i.e., provinces I and III (see Fig. 13), and because of this isolation it is possible that these specimens represent two different species. This possibility is further emphasized by significant differences in the associated faunal populations. In central Pennsylvania, crinoids and *Onniella multisecta* occur with lesser numbers of *Hallopora, Rafinesquina* "*alternata*" and *Sowerbyella* (*Sowerbyella*) *sericea,* which are part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. In southwestern Virginia and northern Tennessee, more numerous specimens of *Hallopora* are found in both the Spiriferid and Orthid Populations of the *Zygospira–Hebertella* Community (see Table 13). Furthermore specimens of *Hallopora* from northern Tennessee localities (see Pl. 9, figs. 1 and 4) have been tentatively identified as a form resembling Lower Richmond species in Kentucky, whereas specimens from central Pennsylvania localities do not resemble these forms and may be slightly older. The significance of a slight decrease in the age of the fauna from north to south has been discussed above.

TABLE 13. The associated faunal elements of *Hallopora* in southwestern Virginia and northern Tennessee. The *Hallopora* faunal association in central Pennsylvania is not listed in this table but discussed in the text.

	Clinch Mt., Tenn.	Lone Mt., Big Ridge, Wallen Ridge, Tenn. Cumberland Mt., Clinch Mt., Rich Mt., Va.
Locality numbers	125, 126	127, 128, 132, 137, 147, 184
Associated faunal elements	*Hallopora* *Batostomella* *Zygospira recurvirostra* *Modiolopsis modiolaris*	*Hallopora–Dekayia* *Zygospira recurvirostra* *Pterinea (Caritodens) demissa* *Hebertella sinuata* *Rafinesquina "alternata"*
Population	Spiriferid	Orthid
Substratum	lime mud	silty mud

BRACHIOPODA
Plates 10-15

Brachiopods are the most numerous and widespread faunal elements in the central Appalachian Upper Ordovician rocks. The phylum is represented by five orders and eight species. There have been only a few recent comprehensive taxonomic reviews of North American Lower Paleozoic Brachiopoda useful to this study; these include Schuchert and Cooper (1932), Salmon (1942), D. Hall (1962) and Williams and Wright (1963). The generic review by Williams et al. (1965) and the studies of predominantly European species by Jones (1928), Bancroft (1928, 1945), Whittington (1938) and Williams (1953, 1962) proved valuable.

PHYLUM BRACHIOPODA
CLASS INARTICULATA
ORDER LINGULIDA
SUPERFAMILY LINGULACEA
FAMILY LINGULIDAE

GENUS *LINGULA*?
Plate 10, figures 1-5

A small to medium-size linguloid shell (over 150 specimens, averaging 15 mm length) is a widespread and common faunal element throughout the central Appalachian Upper Ordovician strata. Unfortunately preservation is so poor that no internal features are known, and hence the precise generic designation must remain in doubt. The linguloid fossils of the North American Ordovician have usually been referred to *Lingula* or *Pseudolingula*, and Bassler (1919, p. 232) introduced the name *Lingula nicklesi* for specimens in the "*Orthorhynchula* Bed" of south-central Pennsylvania. I have collected from this same general region but at present do not feel that these specimens can be shown to be equivalent to *L. nicklesi* from the Ohio Valley (Bassler, 1919, pl. 57, figs. 1-3, figures specimens only from Cincinnati, Ohio). The following list includes possible subjective synonyms.

Pseudolingula iowensis (Owen, 1894)
P. rectilateratis (Emmons, 1842)
Lingula elderi Whitfield 1880
L. quadrata Hall 1847
L. waynesboroensis Foerste 1910
L. cincinnatiensis (Hall and Whitfield, 1875)
L. nicklesi Bassler 1919

Lingula? is numerous from south-central Pennsylvania to southern Virginia, brachiopod faunal province II (Fig. 14), and is most often found with: 1) *Tancrediopsis cuneata*, *Plectonotus*? sp. and *Ischyrodonta truncata*, 2) by itself, and 3) locally with *Orthorhynchula linneyi*. The first two occurrences characterize the Linguloid Population of the *Orthorhynchula–Ambonychia* Community, whereas the third constitutes a portion of the Rhynchonellid Population of the same community. The rock type ranges from muddy silt to a clean sand, and scattered linguloids have been found in hard orthoquartzitic Oswego sandstones. Linguloids are found higher in the upper Reedsville section than any other species, occasionally occurring alone and in significant numbers only a few feet below the contact with the Oswego Sandstone. Figure 31 outlines the general faunal-stratigraphic relationships.

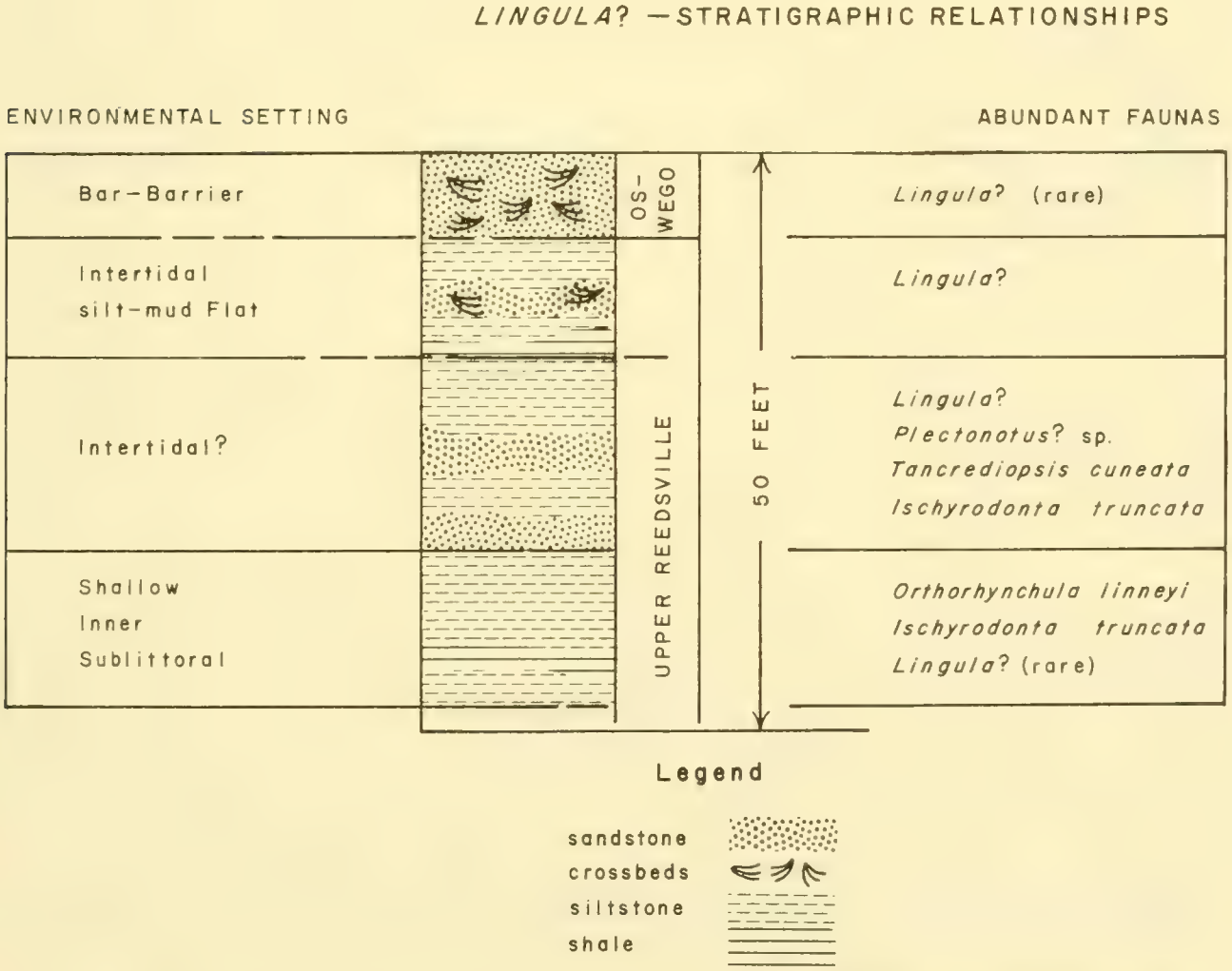


FIG. 31. Associated faunal elements of *Lingula*?. Stratigraphic section is a composite from exposures in south-central Pennsylvania and eastern West Virginia. Lithology schematically presented. *Lingula*? is common only in the environments interpreted as intertidal and silt-mud flat.

The life habits of Recent linguloids, *Lingula* and *Glottidia*, are probably better known than those of any other brachiopods (see Craig, 1952; Hyman, 1959; Rudwick, 1965). Jørgensen (1966, p. 8–10) summarized the suspension feeding mechanism of linguloids. Hyman (1959, p. 589) quotes earlier investigators to the effect that linguloids are very general feeders, their digestive tracts containing a variety of organic and inorganic materials.

Yatsu (1902) has found that Recent linguloids can burrow about a foot below the surface of the substratum and that their pedicle is attached to shell fragments or more consolidated, coarser sediments. I have found definite vertical linguloid burrows in the lower Oswego sandstones, though linguloid burrows need not be vertical. Rudwick (1965, p. H203) felt that this infaunal mode of life was not reflected in any distinctive feature of the shell itself and that many fossil linguloids may have been epifaunal.

The Recent linguloids inhabit shoals, banks, mud-sand flats and beaches; the substratum ranges through muds and coarse sands. Hatai (1940) has found Recent linguloids limited to depths of less than 20 meters with only rare occurrences in deeper waters. Craig (1952, p. 115) added that besides being a shallow water marine animal, the Recent linguloids could probably withstand prolonged periods of brackish water conditions; none have been reported from truly fresh water environments.

Rudwick (1965, p. H212) claimed that few fossil brachiopods could be used as reliable indicators of water depth, with the possible exception of fossil linguloids found without any other associated brachiopods. The latter occurrences could be taken to reflect a possible intertidal environmental setting. I believe that a very nearshore, possibly intertidal, environment is highly likely where linguloids are the single abundant faunal element, and is probable where *Lingula*? occurs with *Tancrediopsis cuneata*, *Plectonotus*? sp. and *Ischyrodonta truncata*. Association with *O. linneyi* probably reflects a shallow sublittoral regime as contrasted to the sheltered mud-silt flats of the other two associations.

One other inarticulate brachiopod, *Schizocrania*, is found in the central Appalachian Upper Ordovician rocks. It is not common, being found at only one locality in a silty mud associated with large *Modiolopsis modiolaris* and a few *Ambonychia praecursa* from the Rynchonellid Population of *Orthorhynchula–Ambonychia* Community (see Table 10). Apparently, it lived in a normal marine, quiet sublittoral environment.

Class ARTICULATA
Order ORTHIDA
Suborder ORTHIDINA
Superfamily ORTHACEA
Family PLECTORTHIDAE
Subfamily PLECTORTHINAE
Genus *HEBERTELLA*

Hebertella sinuata (Hall, 1847)
Plate 11, figures 7-8; plate 12, figures 1-2

Orthis sinuata Hall, 1847, p. 128, pl. 32B, figs. 2a-i, 2k; pl. 32C, figs. 21-s. Meek, 1873, p. 96, pl. 9, figs. 4a-g.

[?]*Orthis subjugata* Hall, 1847, p. 129, pl. 32C, figs. 1a-i, 1k, 1m, 1n.

[?]*Orthis occidentalis* Hall, 1847, p. 127, pl. 32A, figs. 2a-i, 2h, 2l, 2m; pl. 32B, figs. 1a-i. [not] Meek, 1873, p. 96, pl. 9, figs. 3a-h. [not] Hall, 1883, pl. 34, figs. 31-34; pl. 35, figs. 16-21.

Orthis occidentalis var. *sinuata* (Hall). Meek, 1873, p. 98.

Hebertella sinuata (Hall). Hall and Clarke, 1892, p. 222, figs. 1-8. Foerste, 1910, p. 52, pl. 2, fig. 5. Foerste, 1924, p. 110, pl. 10, fig. 11. Butts, 1941, p. 117, pl. 97, figs. 1-4. Cooper, 1944, p. 299, pl. 113, figs. 14-20. Williams and Wright, 1965, p. H324, figs. 205, 5a-e.

Hebertella occidentalis var. *sinuata* (Hall). Cumings, 1908, p. 908, pl. 34, figs. 3, 3a-e. Schuchert and Cooper, 1932, p. 59, pl. 11, figs. 14, 17, 19, 20, 22-26.

[?]*Hebertella occidentalis* (Hall). [not] Hall and Clarke, 1892, p. 222, pl. 5A, figs. 11, 12. [not] Cumings, 1908, p. 906, pl. 34, fig. 4. Foerste, 1910, p. 53, pl. 2, figs. 1a, 1b, 2a, 2b. Foerste, 1924, p. 110, pl. 5, figs. 5a, b; pl. 10, figs. 10a, b. [?] Ruedemann, 1925b, p. 120, pl. 13, figs. 1, 2.

[?]*Hebertella subjugata* (Hall). Foerste, 1910, p. 54, pl. 2, fig. 8. Foerste, 1912, p. 129, pl. 8, fig. 6.

[?]*Hebertella latasulcata* Foerste, 1914b, p. 131, pl. 3, figs. 7a, b.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of moderately large size (median length of 24 specimens, 16 mm; median width of 17 specimens, 23 mm), inequivalved, biconvex, globose, outline subelliptical. Shape only slightly variable, wider than long, greatest width near hinge line, length varying between 62 and 76 per cent of width (median of 12 specimens, 74 per cent). Hinge line long, straight, wide; interarea curved, both valves more or less apsacline. Cardinal angle obtuse; extremities subround. Anterior commissure uniplicate to sulcate; anterior margin broadly curved to flat, or slightly concave; lateral margins subparallel. Multicostellate, costae broad, rounded, numerous; spaces between costae narrow, deep; costellae few, prominent, bifurcation only near valve margins of larger shells; concentric striae faint, very few, widely spaced near valve margins.

Pedicle valve broadly convex, broad sulcus, umbo inflated, beak slightly incurved; delthyrium moderately large, deltidium unknown; delthyrial chamber deep; dental plates extend as elevated ridges anterolaterally to surround ventral muscle scar. Two diductor scars, broad, subcrescentic, not enclosing adductor scar anteriorly; two distinct adductor scars, impression of support on internal mold, double median ridge with shallow central grove; adjustor scars unknown.

Brachial valve sharply convex, wide fold, prominent beak arched over ventral interarea. Notothyrial chamber deep; cardinalia preserved on internal mold; brachiopores at lateral margins of notothyrium, divergent anteriorly, short, pointed. Dental sockets deep. Cardinal process, thick ridge, extends anteriorly part way toward center of valve, myophore prominent. Dorsal muscle scars obscure, two posterior adductors, subovate. Mantle canal system unknown. Shell fibrous, impunctate, possibly endopunctate, irregular pitting of internal surface.

Materials. The description is based on over 45 specimens from central Virginia and northern Tennessee deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Hebertella sinuata* is tentative pending a complete taxonomic review of the North American species of *Hebertella*. *H. sinuata,* the type of the genus proposed by Hall and Clarke (1892, p. 198), comprises a heterogeneous assemblage of orthids. Their definition was subsequently emended by Schuchert and Cooper (1932, p. 59), who should be consulted for outstanding figures of *H. occidentalis* var. *sinuata* (Schuchert & Cooper, 1932, pl. 11, figs. 14, 17, 19, 20, 22-26).

Hall (1847, p. 128), in the original description of *Orthis sinuata,* stated that the misidentification of this and other "similar species" could result from collections of only small amounts of material. He believed that variations related to age were very important. Schuchert and Cooper (1932, p. 60) found that young forms of *Hebertella* could scarcely be distinguished from mature species of *Plectorthis*, either internally or externally.

Within the genus itself uncertainty exists as to assignment of specimens among *H. occidentalis, H. sinuata* and *H. subjugata.* These three eastern North American Upper Ordovician species show only slight differences in external morphology, are commonly listed as occurring at the same horizon (Hall, 1847, p. 130), and have very poorly defined comparative internal features. *H. subjugata* has been usually distinguished from the other two by its finer plications. *H. occidentalis* is supposed to show a slight sulcus near the beak of the brachial valve that distinguishes it from the nonsulcate *H. subjugata* and *H. sinuata.* All previous investigators have admitted that the distinctions are difficult to make. Complete gradations in the shell plications and brachial valve depressions have been noted by Foerste (1910, p. 53) at a number of Upper Ordovician localities in the Ohio River Valley.

Earlier Foerste (1909, p. 224) had described what appears to be a specific difference in the external shell morphology of *Hebertella*; the presence of a pronounced sulcus in the brachial valve, not just a slight depression near the beak. *H. alveata* (cf. *H. alveata* var. *richmondensis*) Foerste 1909 incorporated many of the dorsally sulcate forms that earlier authors had called *Orthis occidentalis.* One of these authors was Meek (1873, p. 98) who remarked that all gradations exist between those specimens that have a well-defined mesial sinus on the dorsal valve (i.e., *H. alveata* Foerste 1909 = *Orthis occidentalis* Meek 1873) and others in which no trace of a sinus can be found [i.e. *H. sinuata* (Hall, 1847)]. Thus it seems that *H. sinuata* must be placed in the category of *nomen inquirendum* pending a restudy of this material.

Very well preserved internal and external molds have been found at a few Upper Ordovician localities in the central Appalachians. A slight mesial sulcus near the beak of the brachial valve has been noted in a few specimens, scattered throughout a number of localities. A distinctive pattern of coarser or finer plications has not been recognized, and none of the extremely sulcate forms have been obtained at any of the central Appalachian localities. The highly sulcate *Hebertella* has been reported only from Upper Ordovician strata of the Ohio River Valley.

Hebertella sinuata is abundant only along the more southeasterly exposures of the Reedsville Formation, south-central Virginia and northern Tennessee, brachiopod faunal province III (see Fig. 14). Specimens tentatively identified by me as *H. sinuata* have been found in the Shochary Ridge Sandstone of eastern Pennsylvania, but gener-

ally poor preservation prevents discrimination from *Plectorthis*. Table 14 lists the commonly associated abundant faunal elements, all part of the *Zygospira–Hebertella* Community. Not included on the table are the eastern Pennsylvania localities where questionable *H. sinuata* occurs with two distinctly northern species of brachiopod faunal province I, the numerous *Onniella multisecta* and *Sowerbyella (Sowerbyella) sericea*, which are part of the *Sowerbyella–Onniella* Community.

TABLE 14. The associated faunal elements of *Hebertella sinuata* in northern Tennessee and sounthwestern Virginia. All brachiopods are part of the *Zygospira–Hebertella* Community.

	Catawba Mt., Vt.	Clinch Mt., Walker Mt., Va.	Powell Mt., Va. Cumberland Mt., Va. & Tenn. Wallen Ridge, Clinch Mt., Tenn.
Locality numbers	177, 179	147, 149, 150	130, 131, 132, 133, 139
Associated faunal elements	*Rafinesquina "alternata"* *Zygospira recurvirostra*	*Zygospira recurvirostra* *Pterinea (Caritodens) demissa* *Hallopora* *Modiolopsis modiolaris* *Orthorhynchula linneyi*	*Zygospira recurvirostra* *Hallopora* *Amplexopora* *Pterinea (Caritodens) demissa*
Substratum	sand–silt	muddy silts	lime muds

The life habits and environmental setting of *H. sinuata* can be inferred from the few studies of Recent brachiopods, even though there are no living orthids. It is assumed that *H. sinuata* thrived in waters of normal marine salinity and was rooted to the silty substratum by a fairly stout pedicle. Attachment in the normal fashion of articulate brachiopods would allow the heavy shelled form with a much more convex brachial valve to rest on or be partially buried in the substratum, the convexity raising the plane of commissure above the ctenidial-fouling, sediment-laden bottom currents. The patchiness of the distribution even in areas where the shells are abundant is common in the other Upper Ordovician brachiopod species and is characteristic of the gregarious nature of Recent brachiopods. The distinctly globose, trilobate form of *H. sinuata*, superficially much like that of *O. linneyi*, may be indicative of adaptation to more turbulent conditions than that experienced by the other central Appalachian orthids, strophomenids and spiriferids. The functional significance of shape is reviewed in the discussion of *O. linneyi*.

The stratigraphic and geographic evidence points to a quiet, but sporadically turbulent, sublittoral habitat for *H. sinuata*. The overall restriction of the fauna to the south may be explained as a function of currents, rates of sedimentation or temperature control. *H. sinuata* is most common in fine sands and silts and appears to replace *O. linneyi* in southwestern Virginia and northern Tennessee, brachiopod faunal province III, as the dominant inner sublittoral brachiopod species. *H. sinuata,* however, gives way to the smaller atrypid *Zygospira recurvirostra* in finer silts and muds of the same geographic region, possibly indicating more sheltered nearshore regions.

Superfamily ENTELETACEA
Family DALMANELLIDAE
Genus *ONNIELLA*

Onniella multisecta (Meek, 1873)
Plate 11, figures 1-6

Orthis multisecta James, 1871, p. 10 (*nomen nudum*). Miller, 1875, p. 22. Sardeson, 1897, p. 97, pl. 4, figs. 20-23.

Dalmanella testudinaria var. *multisecta* Meek, 1873, p. 112, pl. 8, figs. 3a-d, [?]figs. 1a-c. Cumings, 1908, p. 901, pl. 33, figs. 4, 4a-c.

Dalmanella multisecta (Meek). Bassler, 1909, pl. 14, figs. 4-6. Foerste, 1909, p. 217. Bassler, 1919, p. 244, pl. 54, figs. 5, 6. Rudemann, 1925b, p. 117, pl. 12, figs. 1-3. Secrist and Evitt, 1943, p. 367.

[?]*Dalmanella fultonensis* var. *lorrainensis* Ruedemann, 1925b, p. 119, pl. 12, fig. 7.

[?]*Dalmanella fultonensis* var. *rotunda* Ruedemann, 1925b, p. 120, pl. 12, figs. 4-6.

[?]*Dalmanella fertilis* (Bassler). Butts, 1941, p. 113, pl. 96, figs. 3-6.

[?]*Dalmanella emacerata* (Hall). Butts, 1941, p. 114, pl. 96, fig. 16.

Resserella multisecta (Meek). Cooper, 1944, p. 353, pl. 138, figs. 15-18.

Onniella multisecta (Meek). Hall, 1962, p. 148, pl. 20, figs. 11-31.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size (median length of 35 specimens, 8 mm; median width of 31 specimens, 11 mm), slightly inequivalved, generally biconvex, outline subcircular. Shape only slightly variable, wider than long, greatest width near midpoint between hinge line and anterior margin, length varying between 76 and 82 per cent of width (median of 23 specimens, 78 per cent). Hinge line short, straight; interarea curved, both valves orthocline or anacline. Cardinal extremities rounded. Anterior commissure rectimarginate to faintly sulcate; anterior and lateral margins broadly rounded. Multicostellate, costae coarse, broad, rounded; costellae prominent, numerous bifurcations especially near shell margins. Concentric striae of two distinct types: coarse, widely spaced, concentrated near valve margins; fine, numerous, over entire surface of valve.

Pedicle valve broadly convex, umbo inflated, broadly rounded, beak erect. Delthyrium prominent, large, triangular; deltidium unknown; delthyrial chamber deep; hinge teeth large, crural fossettes deep, anterior-inner edge of hinge teeth well preserved on latex impression of internal mold (Pl. 11, fig. 2); dental plates small, extend as faint ridges anteriorly to surround posterodorsal portions of ventral muscle scar. Two diductor scars, elongate, flanking but not entirely enclosing a medial adductor scar.

Brachial valve slightly convex, flattened at margins, broadly sulcate. Notothyrial chamber deep, triangular. Cardinalia preserved on latex impression of internal mold (Pl. 11, fig. 3); brachiopores at lateral margins of notothyrium, diverge anteriorly, short, erect, razor-like, thickened at base where fused to medial ridge; fulcral plates unknown. Denticle small, narrow, forms posteriolateral lip of deep socket. Cardinal process small, bilobed, extends anteriorly toward center of valve as thickened medial ridge. Dorsal muscle scars prominent, quadripartite, paired posterior and anterior

adductors, subround, anterior scars about twice as large as posterior ones. Mantle canal system unknown. Shell microstructure and mineralogy unknown, preservation as internal and external molds.

Materials. The description is based on over 50 specimens from eastern and central Pennsylvania deposited in the Peabody Museum.

Discussion. These central Appalachian Upper Ordovician specimens are assigned to *Onniella multisecta* on the basis of their consistently small size, subcircular outline, well-defined ventral and dorsal muscle scars and delicate cardinal processes. Misidentification as the similar *O. emacerata* or *O. meeki* was avoided, as *O. emacerata* is a much larger shell with a subrectangular outline and *O. meeki*, although exhibiting a good deal of shape variation, has a prominent large cardinal process which fills the notothyrial chamber of the brachial valve and is visible from the exterior.

The Ordovician dalmanellids are one of the more carefully studied brachiopod groups. Unfortunately there has been a general tendency toward genus-making and nomenclatural error since Hall and Clarke (1892) introduced the genus *Dalmanella*, "Group of *Orthis testudinaria*." Subsequent works of particular note are by Bancroft (1928, 1945), Schuchert and Cooper (1932), and the important summary papers of Hall (1962), and Williams and Wright (1963).

Many of the previous investigators of the eastern North American Upper Ordovician rocks undoubtedly have identified specimens of *O. multisecta* as *Dalmanella* (= *Orthis*) *testudinaria*, a European Ordovician species made the type of the new genus *Dalmanella* by Hall and Clarke (1892, p. 205), but so inadequately defined that it soon came to contain a heterogeneous group of North American dalmanellid species. Sardeson (1897), Raymond (1921) and Foerste (1924) presented an increasingly better documented case for the argument that species agreeing with the type *Dalmanella testudinaria* were unknown to North America. Schuchert and Cooper (1932, p. 126), in their monographic review of the dalmanellid genera, unfortunately disregarded the conventions of zoological nomenclature and replaced the type *Dalmanella* (*D. testudinaria*) with the common North American species *Dalmanella rogata*, which was supposed to be the true representative of a widespread Upper Ordovician North American genus. In the process they placed *Onniella* Bancroft, 1928, in synonymy with the emended *Dalmanella*.

Cooper (1942, p. 229) recognized the error but no longer believed the species in the "*Dalmanella rogata* group" were congeneric with Bancroft's *Onniella* and felt that this latter genus in North America was restricted to a few species of Richmond age. This, of course, left the "*Dalmanella rogata* group" without a valid generic designation. Cooper (1944, p. 251–252) subsequently remedied this when he placed the "*D. rogata* group" in the genus *Resserella*. Unfortunately Schuchert and Cooper (1932, p. 126) had emended the definition of *Resserella* Bancroft and had designated a type that placed it in synonymy with *Parmorthis*; the result of this synonymy was to restrict the term *Resserella* to a group of Silurian specimens and again leave the distinctive "*Dalmanella rogata* group" nameless. Cooper (1956, p. 956) thus introduced the new genus *Paucicrura* with its type *Dalmanella rogata* and presumably included in the new genus all those Upper Ordovician species originally congeneric with *Dalmanella rogata*.

Hall (1962) reviewing the Cincinnatian dalmanellids of the Ohio Valley area, placed *Paucicrura* in synonymy with *Onniella*. Hall (1962, p. 139) cited the works of Opik (1933) and Whittington (1938) in considering the Upper Ordovician species of the "*Dalmanella rogata* group" as belonging to the genus *Onniella*. Hall further stated that *Paucicrura* must be placed in synonymy with *Onniella* since the generic descriptions given by Bancroft (1928, p. 55) and Schuchert and Cooper (1932, p. 120) are identical. Because Schuchert and Cooper considered "*Dalmanella*" and *Onniella* to be congeneric and because there is no description of the type for the genus *Paucicrura* given by Cooper (1956), the earlier definition is the only valid one standing. Williams and Wright (1963, p. 28–29) list quite similar diagnostic features for *Onniella* and *Paucicrura* and found only the undifferentiated bilobed cardinal process in *Onniella* to differ from the differentiated trilobate process in *Paucicrura*. Hall (1962), however, found bi-, tri- and quadrilobate cardinal processes in *Onniella*. Howe and Reso (1967, p. 358) submit a reasonable suggestion: if the wide variation of the posterior portion of the cardinal process in *Paucicrura* can be demonstrated, *Paucicrura* should be placed in synonymy with *Onniella*.

The distribution of abundant *O. multisecta*, limited to eastern and central Pennsylvania, brachiopod province I, shows almost the same zoogeographic pattern (see Table 3) as that of *Sowerbyella* (*Sowerbyella*) *sericea* (see Fig. 14). However, *O. multisecta* becomes suddenly sparse in south-central Pennsylvania; only rare, scattered specimens are found in northern Virginia (loc. 160, 161, 162, 165, 167, 168). The enclosing rock is commonly a mud or muddy silt; the abundant associated faunal elements are *Sowerbyella* (*Sowerbyella*) *sericea* and crinoids, part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. In certain locales *Rafinesquina* "*alternata*", *Hallopora* and *Flexicalymene* are common. Infrequently there occur concentrated patches of *Cryptolithus, Sinuites* and *Receptaculites*. *O. multisecta*, like many of the other central Appalachian Upper Ordovician brachiopods, often occurs in highly concentrated patches where entire bedding planes are covered with this one species.

The life habits and environmental setting of *O. multisecta* are as hard to infer as were those for the other orthids and strophomenids. As in the case of the brachiopods, one can assume a normal marine environment, waters of low turbidity and low but sporadic rates of sedimentation. Temperature may be an important factor, as the species was confined to the northeastern parts of the central Appalachians during the Late Ordovician. *O. multisecta* presumably had a fairly stout functional pedicle by which it was attached to the muddy silt substratum, other shells, or non-preservable material such as worm tubes or algae. Considerable organic stain is evident with the dalmanellids. The patchiness and gregarious nature of *O. multisecta* are common in Recent shelf brachiopod faunas and are also usual in the other Upper Ordovician brachiopod species. Geographic and stratigraphic evidence points to a habitat somewhat north of the major area of terrigenous clastic influx, but in all cases the fauna appears to have been abundant only in the sublittoral, probably outer sublittoral, relatively quiet waters dominated by a few numerous, closely bunched species. This shelf portion appears to be assumed elsewhere by *Zygospira recurvirostra* and some *Hebertella sinuata*, brachiopod faunal province III (see Fig. 14), which replace *O. multisecta* southward.

ORDER STROPHOMENIDA
SUBORDER STROPHOMENIDINA
SUPERFAMILY PLECTAMBONITACEA
FAMILY SOWERBYELLIDAE
SUBFAMILY SOWERBYELLINAE
GENUS *SOWERBYELLA*

Sowerbyella (*Sowerbyella*) *sericea* (Sowerby, 1839)
Plate 12, figures 3-6; plate 13, figures 1-4

Leptaena sericea Sowerby, 1839, p. 636, pl. 19, figs. 1, 2a, [?]2. Hall, 1847, p. 110, pl. 31B, figs. 2a-h; p. 287, pl. 97, figs. 3a, 3a*, 3b. [not] Hall, 1852, p. 59, pl. 21, figs. 1a-e. Billings, 1856, p. 41, fig. 2. Billings, 1863, p. 163, figs. 139a-c. Meek, 1873, p. 70, pl. 5, figs. 3a-e, [?]3f-h.

Strophomena sericea (Sowerby). Conrad, 1840, p. 201. Emmons, 1842, p. 394, fig. 105.1. Owen, 1844, p. 269, pl. 105, fig. 1. Emmons, 1855, p. 199, pl. 11, figs. 6a-f.

[?]*Leptaena sericea* var. *rugosa* Meek, 1873, p. 72, pl. 5, figs. 3f-h.

[?]*Leptaena aspera* James, 1874a, p. 151.

Plectambonites sericea (Sowerby). Shaler, 1876, p. 28. Hall and Clarke, 1892, pl. 15, figs. 25, 27-29, [?]26. Winchell and Schuchert, 1895, p. 414, pl. 32, figs. 10-12. Cumings, 1908, p. 922, pl. 36, figs. 1, 1a-c. Bassler, 1909, pl. 14, figs. 1, 2. Parks and Dyer, 1922, p. 35, pl. 7, figs. 15, 16. Foerste, 1924, p. 113, pl. 13, figs. 2a, b, 3. Ruedemann, 1925b, p. 123, pl. 12, fig. 18.

[?]*Plectambonites sericeus* var. *asper* (James). Ruedemann, 1901, p. 18, pl. 1, figs. 6, 7.

[?]*Plectambonites sericeus* var. *typus* Ruedemann, 1912, p. 91, pl. 4, fig. 6, [?]figs. 3, 4, 5.

[?]*Plectambonites rugosa* var. *clarksvillensis* Foerste, 1912, p. 127, pl. 1, figs. 7a, b, [?]7c; pl. 10, figs. 7a-d.

[?]*Plectambonites rugosa* (Meek). Foerste, 1912, p. 123. Bassler, 1919, p. 255, pl. 54, figs. 31-33. [?]Parks and Dyer, 1922, p. 35, pl. 7, fig. 11. Ruedemann, 1925b, p. 123, pl. 12, figs. 19-21.

[?]*Plectambonites curdvillensis* Foerste, 1912, p. 122, pl. 10, figs. 15a, b.

[?]*Plectambonites punctostriatus* Mather, 1917, p. 38, pl. 1, figs. 15-17.

[?]*Plectambonites rugosus* var. *manitoulinensis* Foerste, 1924, p. 113, pl. 4, figs. 4a-d.

Sowerbyella sericea (Sowerby). Jones, 1928, p. 414, pl. 21, figs. 1-4.

[?]*Sowerbyella sericea* var. *soudleyensis* Jones, 1928, p. 417, pl. 21, figs. 5, 6.

[?]*Sowerbyella rugosa* var. *triradiatus* Butts, 1941, p. 113, pl. 96, fig. 9.

[?]*Sowerbyella* sp. Butts, 1941, p. 113, pl. 96, fig. 10.

[?]*Sowerbyella rugosa* (Meek). Butts, 1941, p. 113, pl. 96, figs. 7, 8. Cooper, 1944, p. 335, pl. 128, figs. 42, 43, [?]41.

[?]*Sowerbyella clarksvillensis* (Foerste). Cooper, 1944, p. 335, pl. 128, figs. 39, 40.

[?]*Sowerbyella curdvillensis* (Foerste). Cooper, 1956, p. 780, pl. 201A, figs. 1-13.

[?]*Sowerbyella punctostriatus* (Mather). Cooper, 1956, p. 792, pl. 205C, figs. 9-25, pl. 206D, figs. 14, 15.

Sowerbyella (*Sowerbyella*) *sericea* (Sowerby). Muir-Wood and Williams, 1965, p. H379, figs. 243, 1a-f.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of moderately small size (median length of 25 specimens, 8 mm; median width of 29 specimens, 14 mm), inequivalved, outline subcircular. Shape variable, wider than long, greatest width at hinge line, length varying between 44 and 66 per cent of width (median of 20 specimens, 54 per cent). Hinge line long, straight. Cardinal angle variable, acute with subalations, usually right angle. Anterior commissure rectimarginate. Anterior margin broadly curved; lateral margins rounded, subparallel only near hingeline. Parvicostellate, costae closely spaced, narrow, rounded; costellae numerous, bifurcating, regularly spaced between costae; median ridge on brachial valve faint to absent. Concentric striae faint, widely spaced but crowded near valve margins.

Pedicle valve strongly convex, margins nearly flat. Umbonal region not pronounced; beak only slightly above level of hinge line, posterior margin almost straight; cardinal area anacline. Apical foramen unknown, deltidium or pseudodeltidium unknown. Ventral muscle scars well-defined, bilobate, bounded posterolaterally by dental plates, anteromedially by ridges diverging from short, median septum; two adductors, small deeply impressed at posterior extreme of muscle scar; two diductors broad, shallow impression, divided into two subequal elements by low ridges (Pl. 12, fig. 5; Pl. 13, fig. 2).

Brachial valve flat to gently concave, noticeably concave near valve margins. Cardinalia simple; crural bases curved, narrow, diverging widely from posterior end of cardinal process. Chilidial plates form well-defined submedial septa, broaden toward anterior, diverge slightly, fused with small socket ridges, flat-lying, flanking median septum (Pl. 12, fig. 4). Mantle canal system preserved on internal mold (Pl. 13, fig. 1) of brachial valve, lemniscant, inequidistributate (Pl. 12, fig. 3). Shell fibrous, pseudopunctate, punctae regularly spaced in rows between costellae.

Materials. The description is based on over 40 specimens from eastern and central Pennsylvania deposited in the Peabody Museum.

Discussion. These specimens from the central Appalachian Upper Ordovician rocks are tentatively assigned to *Sowerbyella* (*Sowerbyella*) *sericea* pending a complete taxonomic revision of *Sowerbyella* (*Sowerbyella*) and *Sowerbyella* (*Viruella*). Previous investigators described and figured species and varieties of *Sowerbyella* (= *Leptaena*; = *Plectambonites*) from numerous localities in the Upper Ordovician strata of eastern North America. Many of these species and their varieties were named on the basis of slight variations in length-width ratios or poorly defined differences in surface sculpture.

The Family Sowerbyellidae and many other Upper Ordovician brachiopod families have been intensely studied for their usefulness as potential stratigraphic indicators or guides. In the process artificial taxa were created for the recognition of minute subdivisions of rock units. Earlier authors attempted to define slight differences between forms of *Plectambonites* and at first produced numerous stratigraphically defined varieties of *P. sericea*, which later investigators made into distinct species. Foerste (1912, p. 127) was one of the few who recognized at an early date the hopelessness of this situation when he attempted to redefine *P. sericea* var. *rugosa* (Meek) from the Cincinnatian strata of the Ohio River Valley. Although I have not attempted an exhaustive survey of the morphological variation that exists within and among the many world-wide species of Ordovician and Silurian *Sowerbyella* which are presently

recognized, I have included in the present synonymy those species from the Ordovician of eastern North America that I believe to be likely subjective synonyms of *S.* (*S.*) *sericea* based on a review of previously published plates and descriptions.

Sowerbyella (*Sowerbyella*) *sericea* is abundant only in eastern and central Pennsylvania (brachiopod faunal province I, see Fig. 14). A few specimens are found in northern Virginia (loc. 160, 161, 166, 178), where *S.* (*S.*) *sericea* constitutes only a very scattered, less significant faunal element. Associated faunal elements are *Rafinesquina* "*alternata*" and crinoids, (part of the Strophomenid Population of *Sowerbyella–Onniella* Community), but *S.* (*S.*) *sericea* is just as often found by itself. *Onniella multisecta* and *Hallopora* are less commonly associated faunal elements, and specimens of *Flexicalymene*, *Zygospira concentrica* and *Phragmolites* are rare. *S.* (*S.*) *sericea* is most often found in a muddy silt or fine sand. The distribution throughout Pennsylvania and northern Virginia is notably patchy.

The life habits and environmental setting of *S.* (*S.*) *sericea* must, of course, be inferred from the few studies of living articulate brachiopods and the one possible strophomenid descendant, *Lacazella*. Strophomenid ecology is reviewed in the discussion of *Rafinesquina* "*alternata*", p. 89. *S.* (*S.*) *sericea* adults lived unattached on the sea floor, much like *R.* "*alternata*". Williams (1953, p. 2) stated that the young stages also were probably unattached, the valves resting freely on the muddy silts and sands. A normal marine environment, probably outer sublittoral, in an area of fairly low turbulence is most likely. The reasons for the concentration of *S.* (*S.*) *sericea* immediately to the north of and off the major area of terrigenous clastic influx are not obvious. Possibly it results from the presence of a suitable firm muddy silt substratum and a tolerable temperature regime. The extreme patchiness of the distribution is typical of the Upper Ordovician brachiopods and is well-documented in Recent brachiopod populations. Local current patterns probably accounted for this patchy nature of distribution, as they account for both nutrient distribution and larval dispersal.

Superfamily STROPHOMENACEA
Family STROPHOMENIDAE
Subfamily RAFINESQUININAE
Genus *RAFINESQUINA*

Rafinesquina "*alternata*" (Hall, 1847)
Plate 15, figures 1-6

Strophomena Emmons, 1842, p. 403, fig. 112.2 (*nomen nudum*).
Leptaena alternata Hall, 1847, p. 286, pl. 79, figs. 2f-2l, [not] 2a-2d.
Strophomena alternata (Hall). Emmons, 1855, pl. 17, fig. 2; [?]pl. 11, fig. 3.
[?]*Strophomena alternata* var. *fracta* Meek, 1873, p. 91, pl. 7, figs. 3a-3c.
[?]*Strophomena squamula* James, 1874b, p. 335.
Rafinesquina alternata (Hall). Hall and Clarke, 1892, p. 282, pl. 8, figs. 6, 7, [?]8-11. Hall and Clarke, 1895, pl. 84, [?]figs. 17, 18. Bassler, 1909, pl. 14, fig. 9. Bassler, 1919, p. 265, pl. 57, fig. 8. Foerste, 1924, p. 114, pl. 13, figs. 6a-c. Ruedemann, 1925b, p. 126. Butts, 1941, p. 117, pl. 97, fig. 29.
[?]*Rafinesquina squamula* (James). Hall and Clarke, 1892, p. 283. Foerste, 1914a, p. 264. Bassler, 1919, p. 264, pl. 54, figs. 3, 4; pl. 58, fig. 4.

[?]*Rafinesquina alternata* var. *fracta* (Meek). Cumings, 1908, p. 927, pl. 37, figs. 5, 5a.

[?]*Rafinesquina mucronota* Foerste, 1914a, p. 265, pl. 2, figs. 7a, b. Parks and Dyer, 1922, p. 37. Foerste, 1924, p. 115, pl. 14, fig. 1; pl. 30, fig. 6, 7. Ruedemann, 1925b, p. 129, pl. 12, figs. 16, 17.

[?]*Rafinesquina mucronota* var. *torontonensis* Parks and Dyer, 1922, p. 38, pl. 7, figs. 13, 14, 17.

[?]*Rafinesquina alternata* var. *centristriata* Ruedemann, 1925b, p. 127, pl. 12, figs. 13, 14.

[?]*Rafinesquina alternata* var. *mediolineata* Secrist and Evitt, 1943, p. 363, figs. 13, 14.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of moderately large size (median length of 39 specimens, 23 mm; median width of 25 specimens, 24 mm), inequivalved, concave-convex, U-shaped outline. Shape variable, slightly wider than long, greatest width near hinge line, width varying between 85 and 129 per cent of length (median of 21 specimens, 102 per cent). Hinge line long, straight. Cardinal angle variable, sharply acute with small alations or broadly rounded, obtusely angular. Anterior commissure rectimarginate. Lateral margins subparallel, broadly rounded; anterior lateral margins smoothly curved. Parvicostellate, costae on median part of valve, well-defined, thick; costellae, primary and secondary, bifurcating, highly variable in length, regularly spaced. Concentric striae prominent, two kinds: coarse, widely but regularly spaced; fine, closely spaced, faint.

Pedicle valve convex, very broadly curved; beak prominent, pointed; cardinal area anacline; delthyrium prominent, pseudodeltidium unknown; posteroventral muscle scar small, fan-shaped, faint.

Brachial valve gently concave, flattened near anterior margin; cardinalia fragile, cardinal process small, details unknown, notothyrium prominent. Shell pseudopunctate, punctate, punctae regularly spaced in rows between costellae, preserved on internal mold (Pl. 15, fig. 1).

Materials. The description is based on over 50 specimens from Pennsylvania to Tennessee deposited in the Peabody Museum.

Discussion. These specimens from the central Appalachian Upper Ordovician rocks are tentatively assigned to *Rafinesquina* "*alternata*" pending a complete taxonomic revision of the Upper Ordovician Rafinesquininae. Previous investigators working in the central Appalachians had frequently identified these large, concavo-convex strophomenids with a distinctive costellate pattern as *R.* (= *Leptaena*, = *Strophomena*) *alternata*, or as one of its numerous subspecies. It had become customary to group a wide variety of shells under this term. Foerste (1924, p. 114) commented that the extreme variation in size, outline, convexity and internal structures of this long-ranging Middle to Upper Ordovician species made the catch-all *R. alternata* virtually useless. He informally attempted to restrict *R. alternata* to those large, plate-like Rafinesquininae of the Upper Ordovician (Maysville) in Canada and in doing so placed only Hall's Hudson River Group specimens in synonymy.

Later Salmon (1942, p. 574) emended the definition of *R. alternata* in her study of the Mohawkian Rafinesquininae. Her emended description is based only on Hall's

New York Middle Ordovician (Trenton) specimens, and she suppresses the term *R. alternata* in favor of *R. trentonensis.* In the discussion of *R. trentonensis,* Salmon states that the Upper Ordovician (Cincinnatian) forms previously called *R. alternata* do not conform to the emended definition. These later forms are larger, much more convex, and have much less regular costellae. Interior structures are supposed to be more prominently displayed in the Upper Ordovician specimens, but Salmon does not elaborate on the details. She concludes that these specimens very closely resemble *R. alternata* var. *ponderosa* (Hall).

Salmon's (1942, p. 575) informal designation of all Cincinnatian forms previously called *R. alternata* as *R. ponderosa* is not satisfactory. There are numerous references (see Bassler, 1915, p. 1085) to Upper Ordovician (Maysville) specimens, called *R. alternata* (Hall), *R. alternata* var. *fracta* (Meek) and *R. alternata* var. *centristriata* Ruedemann, which do not resemble *R. alternata* var. *ponderosa*, but rather show closer affinity to *R. trentonensis* (Salmon, 1942, emend.). The material I have collected from the central Appalachian Upper Ordovician also appears to be much more similar to *R. trentonensis* than to *R. ponderosa*, although undoubted *R. ponderosa* has been identified from one locality (loc. 97).

However, use of the term *R. trentonensis* for my central Appalachian Upper Ordovician specimens seems a poor choice: first, because Salmon (1942, p. 573) stated that the Upper Ordovician *Rafinesquina* are not conspecific with those of the Middle Ordovician and second, because her emended definition does not include Hall's New York Hudson River Group (Upper Ordovician) *R. alternata*, which the central Appalachian Upper Ordovician specimens closely resemble. The term *R. alternata* must therefore be placed in the category of *nomen inquirendum*, and I will call the specimens from the Upper Ordovician of the central Appalachians *R.* "*alternata*".

The term *R. alternata* var. *mediolineata* was introduced by Secrist and Evitt (1943, p. 363) for specimens found at Massanutten Mountain, north-central Virginia. I have re-collected from their locality (my locality 167) and have found these specimens to exhibit a prominent median costae much like the New York *R. alternata* var. *centristriata* Ruedemann. I am tentatively placing both these taxa in *R.* "*alternata*", because in all other external morphological features these specimens are similar to the other central Appalachian specimens.

Rafinesquina "*alternata*" is widespread throughout the central Appalachian Upper Ordovician rocks but is most abundant from Pennsylvania to northern Virginia, brachiopod faunal province I (see Fig. 14). It is patchy in its distribution in eastern Pennsylvania (Shochary Ridge), West Virginia and southwestern Virginia. Table 15 lists the associated faunal elements of *R.* "*alternata*" in each region, including populations of the *Sowerbyella–Onniella* Community and the *Zygospira–Hebertella* Community. *R.* "*alternata*" occurs alone or with the strophomenid *Sowerbyella* (*Sowerbyella*) *sericea* and crinoids in the Strophomenid Population of the *Sowerbyella–Onniella* Community which is by far its most common association. Most specimens of *R.* "*alternata*" are found in a muddy silt or fine sand.

Any interpretations of the life habits of *R.* "*alternata*" are hindered not only by our lack of knowledge of the anatomy and ecology of almost all Recent articulate brachiopods, but also by the fact that there are no living representatives of the strophomenids with the possible exception of the thecideid *Lacazella* (Williams, 1953). Elliott (1965, p. H857) believed that the affinities of the order Thecideidina must

TABLE 15. The associated faunal elements of *Rafinesquina "alternata"* from eastern Pennsylvania to northern Tennessee.

	Shochary Ridge, Pa.	Raccoon Mt., Nittany Mt., Tuscarora Mt., Pa.	North Mt., Massanutten Mt., Va.	Catawba Mt., Va.	Big Ridge, Lone Mt., Wallen Ridge, Tenn. Garden Mt., Va.
Locality numbers	4, 15, 28	31, 35, 37 104, 108	160, 166 167, 168	177, 178	127, 128 136, 183
Associated faunal elements	*Sowerbyella sericea* *Onniella multisecta*	Crinoids *Sowerbyella sericea* *Hallopora*	(very sparce) *Sowerbyella sericea* *Onniella multisecta*	*Hebertella sinuata* *Sowerbyella sericea* Crinoids *Zygospira recurvirostra*	*Hebertella sinuata* *Zygospira recurvirostra* *Hallopora* *Dekayia*
Population		Strophomenid		Orthid	
Substratum			sand–silt		muddy silts–lime muds

remain uncertain pending a complete restudy of *Lacazella,* which lives permanently cemented to the substratum by its large, convex ventral valve with the much smaller dorsal valve uppermost (Hyman, 1959, p. 585). Williams (1953) and Rudwick (1965) emphasized the characteristic shell modifications of the strophomenids. The loss of a functional pedicle as shown by the small size of the foramen is critical to any environmental reconstructions. More recent studies by Crickmay (1966, p. 503), who sectioned Upper Ordovician specimens of *R.* "*alternata*" from Ohio, point up the possibility that the apical cavity had no primal opening at all. Whether the pedicle was atrophied early in life or was never functional, the mature shell must have lain free on the substratum. An adaptation to a soft substratum is seen in the concavo-convex shell form which probably developed concurrently with the loss of the pedicle.

All modern articulate brachiopods are limited to waters of normal marine salinity and appear to be tolerant of some turbulence, but less tolerant of actual sediment influx. *R.* "*alternata*" probably was no exception, as it lived on a muddy fine-grained sand and silt substratum, supported only by the gently convex ventral valve. The environmental setting of *R.* "*alternata*" and the other abundant strophomenid, *Sowerbyella* (*Sowerbyella*) *sericea,* was probably quiet water and sublittoral. Both animals would have had considerable difficulty in maintaining themselves unattached where wave or current energies were high. The strophomenid shape is suggestive of some Recent bivalve molluscs; for example, some of the free-living plano-convex pectinoids, such as *Aequipecten irradians* which inhabits enclosed waters where the substratum is soft mud or firm (not shifting) sand (Gutsell, 1931, p. 573). Perhaps a better bivalve analogue is the Recent East Indian anomiid *Placuna placenta* (Hornell, 1909, p. 45–47), which lies freely on the muddy silts in sheltered or quiet water environments. It is strongly concavo-convex and reportedly lies with its hinge line submerged in the sediment; it is extremely common in a muddy silt community.

Order RHYNCHONELLIDA
Superfamily RYNCHONELLACEA
Family RHYNCHOTREMATIDAE
Subfamily ORTHORHYNCHULINAE
Genus *ORTHORHYNCHULA*

Orthorhynchula linneyi (James, 1881)
Plate 13, figures 5-8; plate 14, figures 1-5

Orthis(?) *linneyi* James, 1881, p. 41. Nettleroth, 1889, p. 41 pl. 34, figs. 7-13.

Orthorhynchula linneyi (James). Hall and Clarke, 1893, p. 181, pl. 56, figs. 10-13, 19 (13 labeled as 18). Bassler, 1909, pl. 14, figs. 10-12. Foerste, 1910, p. 24, pl. 3, fig. 10. Foerste, 1912, p. 132, pl. 11, fig. 5. Bassler, 1919, p. 271, pl. 57, figs. 9-12. Ruedemann, 1925b, p. 131, pl. 13, fig. 6. Schuchert and Cooper, 1932, p. 42, pl. 16, figs. 12 ,17, 28-30. Butts, 1941, p. 117, pl. 97, figs. 14-19; p. 119, pl. 97, figs. 39-42. Cooper, 1944, p. 309, pl. 117, figs. 41-47. Cooper, 1956, p. 669, pl. 128F, figs. 32-36. Ager et al., 1965, p. H557, figs. 423.2a-f, 425.3a-c.

Platystrophia ponderosa var. *stevensoni* Grabau, 1913, p. 453, pl. 12, figs. 1-3.

Orthorhynchula stevensoni (Grabau). Cooper, 1944, p. 309. Swartz, 1948, p. 111. Swartz, 1955, p. 82. Horowitz, 1965, p. 10.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of moderately large size (median length of 75 specimens, 19 mm; median width of 110 specimens, 23 mm), inequivalved, subpentagonal. Shape variation negligible, slightly wider than long. Cardinal extremities sub-round. Anterior commissure sulcate. Radial costae pronounced, broadly rounded; interspaces deep, sharply rounded.

Pedicle valve broadly convex, medial sulcus prominent. Umbo very prominent, broad, large, elongate; umbonal region inflated, slopes to cardinal extremities steep. Beak erect, curved; beak ridges prominent, preserved on internal mold. Pedicle foramen medium sized, subangular in outline, deltidial plates unknown. Teeth ridge elevated, blunt. Interarea apsacline; hinge line short, straight.

Brachial valve sharply convex, medial fold prominent. Cardinalia preserved on latex impression of internal mold (Pl. 13, fig. 6), functions as crural base; cardinal process simple vertical blade; sockets narrow, elongate, curved anterolaterally from cardinal process; outer socket ridge high, thin; crura prominent, elongate, fusion with dorsal septum. Musculature unknown. Shell calcite, fibrous with conical markings on inner shell surface, preserved on internal mold.

Materials. The description is based on over 900 specimens from south-central Pennsylvania to northern Tennessee deposited in the Peabody Museum.

Discussion. These specimens from the central Appalachian Upper Ordovician rocks are tentatively assigned to *Orthorhynchula linneyi* pending a more complete taxonomic study. *Orthis*(?) *linneyi* was originally described, but not figured, by James (1881) from specimens from the upper part of the Cincinnati Group in Kentucky. The definition was emended by Hall and Clarke (1893, p. 181), who designated it the type of the new genus *Orthorhynchula.* Since that date *Orthorhynchula linneyi* has been identified by numerous investigators from the Middle Ordovician (Trenton) in Kentucky and Tennessee and the Late Ordovician (Cincinnatian) of the Mid-Continent and central Appalachians.

Specimens of *O. linneyi* have undoubtedly been misidentified as the superficially similar *Rynchotrema capax* or *Platystrophia ponderosa,* although neither of these has the short, straight hinge line or well-defined crura* characteristic of *O. linneyi.* Hall and Clarke (1893, p. 182) and Foerste (1910, p. 25) thought that *O. linneyi* was a characteristic fauna of the south-central Appalachians and was not found north of southwestern Virginia, but Ulrich (1911), Bassler (1919) and Butts (1940) identified *O. linneyi* as a major faunal component of the Upper Ordovician strata throughout the central Appalachians. Swartz (1948, p. 111) renewed the claim that "*O. linneyi*" previously identified from central Pennsylvania to southwestern Virginia was not identical to the typical *O. linneyi* from Kentucky and Tennessee; therefore, he used the term *O. stevensoni.* This name had been introduced by Grabau (1913, p. 453) as a variety of *Platystrophia ponderosa,* which it most certainly is not. Unfortunately Swartz has not attempted to document the specific differences between *O. linneyi* and *O. stevensoni* (Swartz, 1948, p. 111; 1955, p. 82). Horowitz (1965, p. 10, 91) comments that *O. stevensoni* evolved from the earlier (i.e., Middle Ordovi-

*The crura are two processes that extend from the cardinalia forming the posterior basal support for the spirolophous lophophore.

cian) *O. linneyi*, but again there is no mention of what evolutionary adaptations have taken place. I have re-collected from Grabau's *Platystrophia ponderosa* var. *stevensoni* type locality in Walker Mountain (my locality 151) and have found these brachiopods similar to all the other *Orthorhynchula* specimens in the central Appalachian Upper Ordovician rocks. A restudy of this central Appalachian and Mid-Continent material should remove *O. stevensoni* from the category of *nomen inquirendum*.

The classification of rhynchonellid brachiopods is reviewed by Cooper (1959) and summarized by Ager et al. (1965). Schuchert and Cooper (1932, p. 26, 42) referred very briefly to *O. linneyi* in their classical study of the orthids and pentamerids, making a small but important revision of Hall and Clarke's 1893 definition. More important are their figures of *O. linneyi* from the Maysvillian of Kentucky (Schuchert and Cooper, 1932, pl. 16). Compared to the central Appalachian form, the Upper Ordovician specimens from Kentucky are about one-fourth to one-third smaller and somewhat less ovate, but specific differences in the cardinalia appear slight (see also Foerste, 1910, p. 27; Ager et al., 1965, figs. 425.3a, b and Pl. 13, fig. 6, this paper).

The most distinctive parts of the rhynchonellid brachiopod shell are the crura, which are moderately long and assume several distinctive patterns or shapes (Cooper, 1959, p. 7). Unfortunately the crura of many of the Paleozoic genera have yet to be described and figured. The preservation of much of the central Appalachian Upper Ordovician material as steinkerns and the lack of sufficient numbers of serial sections through the shell have prevented an accurate definition of the crura, although a few latex impressions of the internal mold of the brachial valve do give some indication of overall size and shape (Pl. 13, fig. 6). Ager et al. (1965, p. H553), however, claim that the morphology of the crura does not seem as valuable in the classification of the Paleozoic rhynchonellids as it is in the Mesozoic and Tertiary species. Unfortunately, there is very little agreement on which morphological features are the most important. Not only does each investigator appear to prefer to employ his own techniques for identification of features, but these features are usually only those which he views as important. Ager et al. (1965, p. 552) have pictured a bleak future of a proliferation of Paleozoic rhynchonellid genera if the trend is not reversed. Cooper (1959), however, has provided a valuable summary of rhynchonellid classification and also has reviewed the morphological characters that should be considered in the definition of any rhynchonellids.

Orthorhynchula linneyi is one of the most characteristic and abundant fossils in the central Appalachian Upper Ordovician strata. Bassler (1919, p. 272) felt that this species was so well-represented at the Fairview-Maysville horizon in the Appalachian Valley and Ridge Province that he applied the name "*Orthorhynchula* Bed" to these rocks. They are mentioned in numerous subsequent publications as the *Orthorhynchula* Zone of the Reedsville or Martinsburg Formation. Butts et al. (1939, p. 26), Butts (1940, p. 208) and Butts (1945, p. 5) reported that *O. linneyi* could be found from Morristown, Tennessee to Tyrone, Pennsylvania. I have found *O. linneyi* most abundant along the westernmost exposures of the Reedsville Formation from southwestern Virginia to south-central Pennsylvania, especially in brachiopod faunal province II, but specimens also may be common in province III (Fig. 14). It is more scattered and noticeably less abundant away from these areas in the central Appalachians; Ruedemann (1925b, p. 131) has found only one specimen in western New York, and

neither Parks and Dyer (1922) nor Foerste (1914a, 1924) has mentioned it as occurring in the Upper Ordovician rocks of southeastern Canada.

The central Appalachian *O. linneyi* is associated with two distinct faunal populations, i.e., the Rhynchonellid Population of the *Orthorhynchula–Ambonychia* Community and the Orthid Population of the *Zygospira–Hebertella* Community (Fig. 14), and is found in sediments ranging from sands to lime muds. *O. linneyi* is, however, most abundant in slightly muddy sands and silts. Table 16 diagrams the associated faunal elements of *O. linneyi.*

The life habits and environmental setting of the central Appalachian Upper Ordovician specimens of *O. linneyi* can be inferred from the sparse amount of data that has been accumulated on existing genera of rhynchonellids. Hyman, (1959, p. 580), in a brief summation of the work done on Recent Rhynchonellacea, pointed out that the anatomy and shell morphology of some of the genera are fairly well known, but there is little data pertaining to the environmental setting of the rhynchonellids. The overall environmental setting of these Upper Ordovician brachiopods is summarized in the chapter on paleoautecology, p. 36.

The Recent rhynchonellids are characterized by a strong elongate pedicle, spirolophous lophophore, and prominent sulcus and fold. Morse (1902, p. 334) claimed that the unrolled arm tip of the lophophore could actually be extended beyond the margins of the shell. Spicules in the lophophore probably provided support for the extension. *Hemithyris psittacea,* anatomically one of the best known Recent species, has been dredged by Remy (1928) near Jan Mayen Island in the Greenland Sea where in one clump 100 *H. psittacea* had been attached to each other or to pebbles. *H. psittacea* has been found at depths to 2200 meters (Hyman, 1959, p. 599), but is the characteristic circumarctic and circumboreal shelf brachiopod. Hertlein and Grant (1944) have found that the cosmopolitan *H. psittacea* descends into Puget Sound and onto the Oregon coastal waters; DuBois (1916), working in the same area, reported *H. psittacea* to have its maximum abundance from 54 to 160 meters water depth. Thus rhynchonellids form a characteristic shelf fauna, inhabiting quiet water at moderate depths in the outer sublittoral.

O. linneyi is common in the central Appalachian sands and silts and may have been clumped over an extensive area of the inner sublittoral shelf. Between the layers with thickly crowded articulated valves are layers with scattered individuals, possibly indicating some post-depositional reworking or variable rates of deposition, or perhaps representing Late Ordovician distributions which were actually fairly patchy. At a few localities in West Virginia the highest stratigraphic occurrence of *O. linneyi* is marked by worm tubes covering the surface of some valves (Pl. 14, fig. 4). A study of Recent worm borings along the Dutch tidal flats by Boekschoten (1966) has shown occasional concentrated patches of highly bored, loose *Cardium edule* shells that had been washed shoreward along the flats. The less common occurrence of worm tubes at the inhalant openings of *O. linneyi* suggests that a few of these were in living position along the shell bank (Pl. 14, fig. 1). Boekschoten (1966, p. 354) has likewise reported that only 6 per cent of the *Cardium edule* shells show specific borings at only the inhalant opening, and he believes that this sort of occurrence documents infestation in living position. The worm-encrusted *O. linneyi* shells represent the nearest-shore occurrence of this rhynchonellid. *O. linneyi* was probably never intertidal, but apparently could tolerate periods of high sediment influx. The apparent strength of

TABLE 16. The associated faunal elements of *Orthorhynchula linneyi* in south-central Pennsylvania, eastern West Virginia and southwestern Virginia.

	Wills Mt., Jacks Mt., Tussy Mt., Shade Mt., Pa.	North Fork Mt., Va. and W. Va.	Clinch Mt., Walker Mt., Garden Mt., Va.
Locality numbers	63, 78, 112, 98, 99, 87, 111	199, 201, 202, 203	147, 150, 149, 184, 181
Associated faunal elements	alone or with *Ischyrodonta truncata*	*Ischyrodonta truncata* *Ambonychia praecursa* occasionally *Modiolopsis modiolaris*, *Dekayia*, *Lingula*?	*Hebertella sinuata* *Ambonychia cultrata* occasionally *Modiolopsis modiolaris*, trepostomatous Bryozoans, *Zygospira recurvirostra*
Population	Rhynchonellid		Orthid
Substratum	sand–silt	muddy silt–silt	muddy silt

the pedicle and the prominent zig-zag valve edges may have provided the necessary support and efficient protective sensory device for this rhynchonellid to exist in a turbulent environment. Rudwick (1964) claimed that the presence of a zig-zag commissure did not imply any special environmental conditions. But judging from the abundance of *O. linneyi* in the silts and sands, the zig-zag opening could be an advantage. This type of opening is also found in *Hebertella sinuata,* which replaces *O. linneyi* to the south in the muddy silts and sands.

There are only minor changes in the shape of the *O. linneyi* shell from West Virginia to northern Tennessee. The larger, more rounded shape in the north gives way to a more elliptical and smaller shell in the south, this change coinciding with a dramatic change in the abundant faunal elements. *O. linneyi* is much less common in the lime muds of the south than in the sands and silts of the north. Thus change in shape may be directly related to local environmental controls. Ager (1965) and Rudwick (1965) discuss some aspects of brachiopod morphology as it relates to the type of substratum, but little is actually known about the adaptive morphology of brachiopods. DuBois (1916) has conducted the only successful experiments on phenotypic variation in brachiopod shells as related to current energy. He found that the valves of *Terebratalia transversa* became shorter and more convex where currents were consistently stronger. Unfortunately this type of experimentation has not been continued. It would appear that the more convex northern forms of *O. linneyi*, abundant in the sands and silts, had been subjected to consistently stronger current energies than the ones in the lime muds of the south.

The overall distribution of *O. linneyi* and its possible mode of dispersal have been briefly touched upon by Ulrich (1911, p. 514), Ruedemann (1925b, p. 131–132) and Horowitz (1965, p. 93), who agree that *O. linneyi* is found only in Tennessee and Kentucky in the Middle Ordovician. It appears to have migrated northward during the Late Ordovician along the western edge of the central Appalachians as far north as central Pennsylvania, with a few scattered occurrences in New York. Horowitz (1965) also believed that the rates of evolution were rapid enough for the change of *O. linneyi* into a distinct Late Ordovician species, *O. stevensoni.*

Order SPIRIFERIDA
Suborder ATRYPIDINA
Superfamily ATRYPACEA
Family ATRYPIDAE
Subfamily ZYGOSPIRINAE
Genus *ZYGOSPIRA*

Zygospira modesta (Hall, 1847)
Plate 14, figures 6-7

Producta modesta Say, MS (*nomen nudum*).

Atrypa modesta Hall, 1847, p. 141, pl. 33, fig. 15; p. 289. Emmons, 1855, p. 192, pl. 10, fig. 15.

Zygospira modesta (Hall). Hall, 1862a, p. 154, figs. 1, 2. Hall, 1867, p. 267, fig. 12. Meek, 1873, p. 125, pl. 11, figs. 4a-d. Hall and Clarke, 1893, p. 155, figs. 146-149; pl. 54, figs. 8-10, 12, [?]7. Winchell and Schuchert, 1895, p. 467, pl. 34, figs. 42-

44. Cumings, 1908, p. 946, pl. 36, figs. 8, 8a-i. Foerste, 1910, p. 29, pl. 2, figs. 15a, b. Bassler, 1919, p. 274, pl. 54, figs. 20-22; pl. 57, figs. 13-16. Parks and Dyer, 1922, p. 40, pl. 7, figs. 19, 22. Foerste, 1924, p. 127, pl. 10, figs. 21a, b. Ruedemann, 1925b, p. 133, pl. 13, fig. 16. Butts, 1941, p. 118, pl. 97, fig. 28. Secrist and Evitt, 1943, p. 367. Cooper, 1944, p. 317, pl. 120, fig. 72. Boucot et al., 1965, p. H634, fig. 518.2a.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size (median height of seven specimens, 6 mm; median width of five specimens, 8 mm), slightly inequivalved, inflated, biconvex, outline elliptical. Shape variation negligible, slightly wider than long, greatest width near midpoint between hinge line and anterior margin. Hinge line short, straight; interarea of both valves, slightly anacline. Cardinal extremities broadly rounded. Anterior commissure uniplicate to strongly sulcate; anterior margin flattened, lateral margins broadly rounded. Costellate, costae subangular, prominent, numbering about 20; costellae faint, one dorsal, arising from bifurcation of median costae, at anterior margin.

Pedicle valve sharply convex, umbo carinated, broad; beak erect, incurved; pronounced fold umbo to anterior margin, margin moderately concave, four costae on fold, inner two larger; foramen unknown, deltidial plates unknown. All internal features of ventral valve unknown.

Brachial valve broadly convex; sulcus deep, margins convex; three costae in depression, central one large, prominent, flanked by faint, thin costae. All internal features of dorsal valve unknown. Shell microstructure and mineralogy unknown.

Materials. The description is based on about 20 specimens from central Pennsylvania and northern Virginia deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Zygospira modesta* is tentative pending a complete taxonomic review of the North American Lower Paleozoic atrypids. *Z.* (= *Atrypa*) *modesta* was first described and figured by Hall (1847), who subsequently (Hall, 1862a) designated it as the type of the genus *Zygospira*. It is the most common and widespread North American Upper Ordovician *Zygospira* and, I believe, has been occasionally confused with *Z. recurvirostra* and *Z. cincinnatiensis*.

The confusion between *Z. recurvirostra* and *Z. modesta* is reviewed in the discussion of *Z. recurvirostra*, p. 99. *Z. cincinnatiensis*, as originally defined by Meek (1873, p. 126) and elaborated upon by Foerste (1910, p. 29), is quite distinct from *Z. modesta* and is not just a larger form, as many investigators have implied. The much coarser, broadly bifurcating costae and the notably elongated anterior margin at the fold and sulcus are, at least, specifically distinct.

Zygospira modesta is found only in central Pennsylvania and northern Virginia, brachiopod faunal province I (see Table 3; also Fig. 14) and is never as abundant as the congeneric *Z. recurvirostra* in the south, brachiopod faunal province III. In central Pennsylvania *Z. modesta* is found in a fine silt to muddy silt, usually with crinoids and at some locales *Isotelus* and *Flexicalymene*, part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. Rare specimens occur in northern Virginia with *Sowerbyella* (*Sowerbyella*) *sericea* and *Rafinesquina* "*alternata*". It is found as far south as central Virginia (loc. 177, 178) where there are a few specimens

in a fine silt-sand dominated by *Hebertella sinuata* of the Orthid Population of the *Zygospira–Hebertella* Community.

Z. modetsa may have differed very little from *Z. recurvirostra* in life habits and environmental setting, and both probably occupied an outer sublittoral regime. The geographic location, brachiopod faunal province I (Fig. 14), and stratigraphic position (Fig. 15) of *Z. modesta* emphasize its outer sublittoral habitat on a muddy silt bottom (see p. 84 and 91 for environmental interpretations of the stratigraphically higher orthids and strophomenids in central Pennsylvania).

Another species of *Zygospira* has been identified in east-central Pennsylvania, brachiopod faunal province I (loc. 120). It is *Z. concentrica* (Ulrich, 1897, p. 14; see Ruedemann, 1925b, p. 134), which is very rare in a black to gray muddy silt dominated by *Onniella multisecta*, *Cryptolithus* and a few specimens of *Sinuites* and *Sowerbyella* (*Sowerbyella*) *sericea*, part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. This association and the substratum type again seem to indicate a quiet, outer sublittoral environmental setting.

Zygospira recurvirostra (Hall, 1847)
Plate 14, figures 8-9

Atrypa recurvirostra Hall, 1847, p. 140, pl. 33, figs. 5a-d. Emmons, 1855, p. 191, pl. 10, figs. 5a-d.

Rhynchonella recurvirostra (Hall). Billings, 1863, p. 168, fig. 152.

[?]*Zygospira modesta* var. *kentuckiensis* James, 1878, p. 7.

[?]*Zygospira kentuckiensis* (James). Nettleroth, 1889, p. 138, pl. 34, figs. 21-25. Hall and Clarke, 1893, p. 157, pl. 54, figs. 11, 15, 16. Foerste, 1924, p. 127, pl. 10, figs. 20a-c; pl. 15, figs. 1, 2a-b, 4a-c. Butts, 1941, p. 117, pl. 97, figs. 5-7. Cooper, 1944, p. 317, pl. 120, figs. 54, 55.

Zygospira recurvirostra (Hall). Hall and Clarke, 1893, p. 157, pl. 54, figs. 1-6. Beecher and Schuchert, 1893, p. 77, pl. 10, figs. 7-21. Schuchert, 1893, p. 82, pl. 11, figs. 1-10, Winchell and Schuchert, 1895, p. 466, pl. 34, figs. 38-41. Ruedemann, 1901, p. 27. Weller, 1903, p. 161, pl. 10, figs. 23-26. Bassler, 1909, pl. 7, figs. 4-5. Foerste, 1914b, p. 132, pl. 1, figs. 2a-c. Bassler, 1919, p. 272, pl. 42, figs. 9-12. Butts, 1941, p. 99, pl. 92, [?]fig. 10; p. 100, pl. 92, fig. 23; p. 118, pl. 97, figs. 34-38. Cooper, 1944, p. 317, pl. 120, fig. 56. Cooper, 1956, p. 673, pl. 142H, figs. 34-38. Boucot et al., 1965, p. H364.

[?]*Zygospira meafordensis* Foerste, 1924, p. 128, pl. 15, figs. 3a-c.

[?]*Zygospira recurvirostra* var. *aequivalvis* Twenhofel, 1927, p. 214, pl. 19, figs. 10-12.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size (median length of 13 specimens, 8 mm; median width of 9 specimens, 9 mm), slightly inequivalved, biconvex, inflated, outline subcircular. Shape variation negligible, length and width almost equal, greatest width near midpoint between hinge line and anterior margin. Hinge line short, straight; interarea of both valves orthocline. Cardinal extremities rounded. Anterior commissure sulcate to uniplicate; anterior margin flattened, lateral margins broadly rounded. Costellate, costae subround, well-defined, numbering 19 to 24; costellae, one dorsal, two ventral, arising from bifurcation of median costae, near anterior margin, more pronounced on ventral fold.

Pedicle valve sharply convex; umbo carinated, narrow; beak erect, incurved; pronounced fold, extending umbo to anterior margin, margins moderately concave, four costae on fold, two on slopes of fold. Foramen mesothyridid, deltidial plates conjunct. All internal features of ventral valve unknown.

Brachial valve broadly convex; sulcus wide, flattened, margin slightly convex to flattened, three costae in depression, two on flanks of depression. All internal features of dorsal valve unknown. Shell fibrous, calcite.

Materials. The description is based on about 30 specimens from southwestern Virginia and northern Tennessee deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Zygospira recurvirostra* must be considered tentative pending a more complete taxonomic survey of the North American Lower Paleozoic atrypids. The central Appalachian material does not preserve any internal structures and has permitted comparisons to be made only on external configuration. Species of *Zygospira* have, however, been previously defined primarily on the basis of size, shape and ornamentation. The taxonomic significance of these characters in *Zygospira* has yet to be critically explored.

Zygospira recurvirostra has long been confused with *Z. modesta,* a very common Upper Ordovician species, which is the type of *Zygospira. Z. recurvirostra* has been previously distinguished from *Z. modesta* by its broader, more shallow mesial depression in the brachial valve, and the five equisized primary costae within the depression (Foerste, 1914b, p. 132; Cooper, 1956, pl. 142H; cf. Pl. 14, fig. 8 in this paper). *Z. modesta,* although about the same size as *Z. recurvirostra* and exhibiting the same total number of costae (about 20), has a much more pronounced, deeper mesial sulcus; the costae within the depression are notably more angular, and of the five costae within the depression the medial one is considerably broader than those on either side, which are characteristically faint (Pl. 14, fig. 7).

The central Appalachian Upper Ordovician specimens can be segregated into what appear to be internally consistent species groups on the basis of this mesial depression. Some criteria previously employed in discriminating between the two groups were found to exist in both. The total number of costae was not significantly different between the species, and the bifurcation of one or two medial costae near the anterior margin occurs in both. This bifurcation of medial costae was previously thought to be diagnostic of *Z. cincinnatiensis* (Foerste, 1910, p. 31), but appears to be common throughout the genus *Zygospira.* Meek (1873, p. 126), Cumings (1908, p. 945), Parks and Dyer (1922, p. 41) and Ruedemann (1925b, p. 134) have described the figured specimens of *Z. cincinnatiensis,* which I have not found in the central Appalachian Upper Ordovician strata. *Z. cincinnatiensis* appears to be a distinct species, although figures identified as *Z. cincinnatiensis* by Hall and Clarke (1895, pl. 54) and Foerste (1910, pl. 6) closely resemble *Z. modesta.*

Zygospira kentuckiensis, initially described by James (1878) from the Upper Ordovician of Kentucky, was thought to resemble closely *Z. modesta,* differing mostly by its larger size. Subsequent descriptions and figures of *Z. kentuckiensis* show a much closer resemblance to *Z. recurvirostra,* though *Z. kentuckiensis* is normally one and a half times larger than *Z. recurvirostra* (Foerste, 1924, p. 127). Some central Appalachian Upper Ordovician specimens which are as large as previously described *Z.*

kentuckiensis show no external morphological differences from the smaller *Z. recurvirostra* with which they are found.

Zygospira recurvirostra is found abundantly only in southwestern Virginia and northern Tennessee, brachiopod faunal province III (Fig. 14), in rock types varying from lime muds to muddy silts. But *Z. recurvirostra* is more characteristic of the finer grade substratum and is found with three distinct but intergrading local faunas which are all part of the Spiriferid Population of the *Zygospira–Hebertella* Community (Table 17).

TABLE 17. The associated faunal elements of *Zygospira recurvirostra* in northern Tennessee and southwestern Virginia. All species are part of the Spiriferid Population of the *Zygospira–Hebertella* Community.

	Lone Mt., Clinch Mt., Tenn.	Clinch Mt., Tenn. Powell Mt., Va. Cumberland Mt., Va.	Powell Mt., Clinch Mt., Va.
Locality numbers	125, 126, 127	131, 141, 133, 135	139, 145, 147, 149
Associated faunal elements	*Murchisonia*?	*Pterinea (Caritodens) demissa*	*Hebertella sinuata*
	Hallopora	*Ambonychia cultrata*	*Pterinea (Caritodens) demissa*
	Batostomella	*Modiolopsis modiolaris*	
Substratum	lime mud	muddy silt–silt	muddy silt–silt

The life habits and environmental setting of *Z. recurvirostra* are at least as indefinite as those of the species of strophomenids and orthids. Probably occupying a normal marine environment, *Z. recurvirostra* lived on a variety of substrata, apparently preferring muds, and was supported by a functional pedicle. Distribution could have been controlled by water turbulence and by sediment influx. The orthid *Hebertella sinuata* noticeably begins to outnumber *Z. recurvirostra* in the fine sands and silts of southwestern Virginia. Thus, *Z. recurvirostra* appears to prefer a quiet water, shelf environment, probably outer sublittoral, though it may have also occupied an inner sublittoral environment in the southern part of its distribution, where there was little terrigenous influx.

GASTROPODA
Plates 16-19

Gastropods constitute a numerically important and widespread faunal element throughout the central Appalachian Upper Ordovician strata. Bellerophontacean, pleurotomariacean and murchisoniacean gastropods are most abundant, but the small amount of well-preserved material and the lack of recent studies of the Lower Paleozoic gastropods have permitted only tentative identification of much of the Appalachian material. Dr. Ellis Yochelson of the U. S. Geological Survey has provided invaluable guidance in the taxonomic assignment of these specimens.

Ulrich and Scofield (1897) have presented the only systematic review of the North American Lower Paleozoic Gastropoda. There has been little attempt to revise their systematics, although Foerste (1914a, 1924), Ruedemann (1926), Secrist and Evitt (1943) and Wilson (1951) have made valuable contributions.

PHYLUM MOLLUSCA
CLASS GASTROPODA
ORDER ARCHAEOGASTROPODA
SUBORDER BELLEROPHONTINA
SUPERFAMILY BELLEROPHONTACEA
FAMILY BELLEROPHONTIDAE
SUBFAMILY PLECTONOTINAE
GENUS *PLECTONOTUS*

Plectonotus? sp.
Plate 17, figures 1-9

DESCRIPTION BASED ON SPECIMENS FROM THE CENTRAL APPALACHIAN UPPER ORDOVICIAN. Shell of small size (median diameter through the coil of 184 specimens, 6 mm; median width of 112 specimens, 3 mm), bilaterally symmetrical. Whorl profile trilobate, preserved as internal mold (Pl. 16, figs. 4, 5); median lobe prominent, arched or sharply convex; lateral lobes narrow, rounded. Aperture unknown. Umbilical sutures sharply defined, prominent shoulder above each umbilicus. Spiral band at whorl periphery preserved on latex impression of external mold, broad, raised, flat (Pl. 16, fig. 3); lunulae unknown. Surface sculpture growth lines fine, paired, intersection with spiral band sharp, swept backwards. All internal features unknown. Shell mineralogy and microstructure unknown.

MATERIALS. The description is based on over 500 specimens from south-central Pennsylvania to west-central Virginia deposited in the Peabody Museum.

DISCUSSION. Assignment of these central Appalachian specimens to *Plectonotus* sp. is tentative. Preservation as internal molds is most common; only one latex impression of an external mold was obtained (Pl. 16, fig. 3). A knowledge of the external characteristics is extremely important in the classification of bellerophontacean gastropods as well as of all other Archaeogastropoda. The single most important criterion for identification of the Bellerophontidae is the presence of an exhalant channel slit that generates a sweeping of growth lines, forming a peripheral spiral band called a selenizone. Boucot and Saul (1963) have reviewed the criteria for identification of a selenizone. The central Appalachian specimens exhibit this sweeping of growth lines which seems to indicate a fairly strong re-entrant angle along with a "U"-shaped sinus. The slit appears to have been narrow, but its length is unknown.

Although there are no living Bellerophontacea, Recent anatomical analogues can be found in the Pleurotomariacea (Yonge, 1947). The re-entrant notch or slit in the outer lip directs exhalant water currents passing out of the mantle cavity and is expressed in the soft anatomy by the presence of two subequal, bipectinate aspidobranch ctenidia. This fact, extrapolated into the fossil record, makes the presence or absence of the slit and the depth of the re-entrant a critical taxonomic character.

Knight, Batten and Yochelson (1960, p. I175) considered *Plectonotus* Clarke a subgenus of the sinuitid genus *Bucanella*. Figured and described by Knight (1941, p. 255–256), *Bucanella* is a trilobate bellerophontacean, characterized by a well-developed sinus but lacking a slit. Clarke (1899), in his original designation of the genus *Plectonotus*, suspected that his material had both sinus and slit; the probable slit-bearing selenizone was so poorly preserved that the later authors decided to make

Plectonotus a subgenus of the non-slit-bearing, but superficially trilobate, *Bucanella*. Recent findings by Boucot and Saul (1963, p. 1046–1047) and Boucot and Yochelson (1966, p. A7–A8) have uncovered a definite slit-bearing, trilobate bellerophontacean gastropod which they have assigned to the genus *Plectonotus*, at the same time removing it from the Sinuitidae and placing it in the Bellerophontidae.

However, as redefined by Boucot and Yochelson (1966, p. A7), *Plectonotus* is confined to beds of Early to Middle Devonian age. The genus shows some affinities to Ordovician and Silurian trilobate bellerophontacean forms, but these earlier genera are poorly understood. It is possible that many of the Silurian specimens referred to *Bellerophon trilobatus* Sowerby [see also *Sinuites* (= *Bellerophon*) *globularis* Miller and Faber 1894, p. 28, pl. 1, figs. 21, 22] are slit-bearing plectonotid-like forms. In fact, that they show a cross-section characterized by a high median lobe much like that of these central Appalachian Upper Ordovician specimens. No presently defined Ordovician bellerophontid with a slit resembles this central Appalachian form; therefore, it is possible that further study will allow an extension downward of the range of the Lower Devonian (?Silurian) genus *Plectonotus* or the introduction of an earlier slit-bearing genus into the subfamily Plectonotinae Boucot and Yochelson, 1966.

The central Appalachian Upper Ordovician *Plectonotus*? sp. is abundant in West Virginia and south-central Pennsylvania. Figure 16 shows the bellerophontaceans to be common only along the western edge of the Reedsville exposures, gastropod faunal province II; *Plectonotus*? sp. is the most numerous representative of this superfamily. The associated faunal elements are *Tancrediopsis cuneata* and *Lingula*? with lesser numbers of *Ischyrodonta truncata*, all part of the Linguloid Population of the *Orthorhynchula–Ambonychia* Community. The enclosing sediment is a muddy silt to fine sand, usually with a high organic content. Phosphate grains, many of which are thought to be partial internal fillings of the *Plectonotus*? sp. shells, are common at some locales. The sediment is often so thoroughly reworked that there are only remnant laminae (Pl. 1).

Subfamily BUCANIINAE

Genus *BUCANIA*

Bucania sp.

Plate 16, figures 10-11; plate 17, figures 1-3

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium to large size (median diameter through the coil of 17 specimens, 14 mm; median width of 8 specimens, 9 mm), bilaterally symmetrical. Whorl profile rounded, broadly arched. Aperture expanded, slightly wide. Umbilicus widely open. Spiral band at whorl periphery faint, preserved as internal mold, bordered by thin flanges (Pl. 17, fig. 1); lunulae unknown. Surface sculpture growth lines very faint, striae normal to anterior margin unknown. All internal features unknown. Shell mineralogy and microstructure unknown.

Materials. The description is based on about 30 specimens from south-central Pennsylvania and West Virginia deposited in the Peabody Museum.

Discussion. The assignment of these Upper Ordovician specimens to *Bucania* sp. was

made with the aid of plates and descriptions given by Knight (1941), Reed (1920), Wilson (1951) and Ulrich and Scofield (1897). The poor preservation of the central Appalachian material and the lack of Recent Lower Paleozoic gastropod studies allows only a tentative assignment (see *Bellerophon cincinnatiensis* Miller and Faber, 1894, p. 29, pl. 1, figs. 23, 24).

Knight, Batten and Yochelson (1960, p. I180) noted that of all the slit-bearing bellerophontid genera, only *Tetranota* shows a superficial resemblance to *Bucania*. *Tetranota* is rare in the central Appalachian Upper Ordovician rocks and has been positively indentified at only one locality in northern Tennessee (loc. 133). *Bucania* sp. is common only in south-central Pennsylvania and is rare in West Virginia and west-central Virginia, gastropod faunal province II and part of I (see Table 3 for localities and Fig. 16).

Bucania sp., although geographically localized, is not everywhere associated with the same faunal elements. In contrast to the more numerous *Plectonotus*? sp., the only other common bellerophontid, it is not limited exclusively to the western parts of the Reedsville exposures, but occurs across the entire width of the Valley and Ridge Province in south-central Pennsylvania. The wider-ranging *Bucania* sp. occurs more frequently, however, with the Linguloid Population than with the Rhynchonellid and Strophomenid Populations (Table 18).

TABLE 18. The associated faunal elements of *Bucania* sp. in south-central Pennsylvania and northern Virginia.

Population	Linguloid Population of the *Orthorhynchula-Ambonychia* Community	Rhynchonellid Population of the *Orthorhynchula-Ambonychia* Community	Strophomenid Population of the *Sowerbyella-Onniella* Community
Associated faunal elements	*Plectonotus*? sp. *Tancrediopsis cuneata* *Lingula*? *Ischyrodonta truncata*	*Orthorhynchula linneyi* *Modiolopsis modiolaris* *Maclurites*? *Trochonema*	crinoid *Onniella multisecta* *Sowerbyella* (*Sowerbyella*) *sericea* *Loxoplocus* (*Lophospira*) *abbreviata* *Sinuopea*?

The geographic distribution of *Bucania* sp. is believed to be primarily limited by the availability of food and by substratum firmness. *Bucania* sp. is abundant only where the sediment is composed of a fine sand or silt, and the genus is extremely rare to the south where muds begin to constitute a greater percentage of the sediment. The substratum had to be hard or firm and the bottom waters only slightly turbid in order to allow for the proper functioning of the aspidobranch gill.

The one characteristic that distinguishes *Bucania* sp. from *Plectonotus*? sp. is its larger size. *Plectonotus*? sp. appears to have been small enough to have lived and browsed on algae, but the larger *Bucania* sp. may have been too large and heavy to be permanently supported by the algal fronds, unless it existed on that part of the frond which was continually submerged. If this was not the case or if the buoyant effect of the water was not able to offset its weight, *Bucania* sp. may have had to rely more on plant detritus accumulating on the surface of the substratum. Clumping of the plant detritus is likely and thus may explain in part the characteristic patchy distribution of *Bucania* sp., even at localities where it is most numerous.

Suborder PLEUROTOMARIINA
Superfamily PLEUROTOMARIACEA
Family LOPHOSPIRIDAE
Subfamily RUEDEMANNIINAE
Genus *RUEDEMANNIA*

Ruedemannia? *lirata* (Ulrich and Scofield, 1897)
Plate 18, figures 1-2

[?]*Murchisonia uniangulata* var. *abbreviata* Hall, 1847, p. 304, pl. 83, figs. 2a, 2c; [?]2b, 2d.

[?]*Pleurotomaria semele* Hall 1861, p. 36.

Lophospira (*?Seelya*) *lirata* Ulrich and Scofield, 1897, p. 988, pl. 72, figs. 56, 59.

Lophospira (*?Seelya*) *lirata* var. *obsoleta* Ulrich and Scofield, 1897, p. 989, pl. 72, figs. 58; [?]57.

[?]*Plethospira semele* (Hall). Ulrich and Scofield, 1897, p. 1010, pl. 70, figs. 8, 9; [?]10.

[?]*Ruedemannia abbreviata* (Hall). Foerste, 1914a, p. 311.

Ruedemannia lirata (Ulrich and Scofield). Foerste, 1914a, p. 312. Knight, 1941, p. 303, pl. 33, figs. 3a, 3b. Knight, Batten and Yochelson, 1960, p. 1209, fig. 121.1.

Lophospira (*Ruedemannia*) *lirata* (Ulrich and Scofield). Bassler, 1919, p. 295, pl. 55, figs. 5, 6.

[?]*Lophospira lirata* (Ulrich and Scofield). Ruedemann, 1926, p. 67.

[?]*Plethospira quadricarinata* Ruedemann, 1926, p. 71, pl. 9, figs. 2, 5; [?]3, 4.

[not]*Lophospira abbreviata* (Hall). Ruedemann, 1926, p. 65, pl. 8, fig. 12; [?]11, 13.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size (height of two specimens, 10 mm and 17 mm), turbiniform. Whorl profile slope about 30 degrees from vertical; whorl surface broadly rounded, two spiral threads; one thread on upper surface raised, rounded, midway between suture and whorl periphery, surface above thread steeply inclined to vertical, concave; another thread below whorl profile, less prominent. Aperture unknown. Umbilicus unknown. Sutures prominent. Spiral bands at whorl periphery rounded, usually three; outline of selenizone prominent, wide, slightly concave; U-shaped sinus broad. Surface sculpture growth lines fine, closely spaced, swept strongly backwards, almost tangential with outer spiral bands; lunulae gently concave forward. All internal features unknown. Shell mineralogy and microstructure unknown.

Materials. The revised description is based on about 10 well-preserved specimens from north-central Pennsylvania deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to the genus *Ruedemannia* is tentative. Foerste (1914a, p. 312) formally designated *Lophospira lirata* Ulrich and Scofield, 1897, as the type of the new genus *Ruedemannia*, which was characterized by subrotund whorls and a trilineate and bilineate peripheral band. Ulrich, however, had figured both trilineate and bilineate *L. lirata* (Ulrich and Scofield, 1897, pl. 72). Foerste (1924, p. 211) subsequently revised his definition of *Ruedemannia* to include those rotund *Lophospira* forms

that Ulrich had placed in his *L. robusta* group (Ulrich and Scofield, 1897, p. 963). But Foerste expressed uncertainty that *R. lirata* was part of the *L. robusta* group. The term *Ruedemannia* was discarded by Ruedemann (1926, p. 67) in favor of *Lophospira.*

Knight (1941, p. 87) thought that *L. robusta* and *L. lirata* were congeneric and included both in the genus *Ruedemannia.* Knight (1941, p. 303) and Knight, Batten and Yochelson (1960, p. I207–209) again defined the genus *Ruedemannia* and seemed to place the major emphasis on the presence of a "U"-shaped sinus and a well-defined slit, whereas they described *Loxoplocus* (*Lophospira*) as having a "V"-shaped sinus and only a short notch, if a notch be present at all. As in the bellerophontacean gastropods, the character of the slit reflects taxonomically important differences. The rotund whorl profile also appears to be in direct contrast to the more angular profile of *Loxoplocus* (*Lophospira*). Yochelson (personal communication), however, believes that the genus *Ruedemannia* must be placed in the category of *nomen inquirendum*; the quality and amount of material studied and the lack of recent taxonomic studies do not permit the genus to be clearly distinguished from *Loxoplocus* (*Lophospira*).

Thus I have used the term *Ruedemannia*? *lirata* for rotund central Appalachian Upper Ordovician pleurotomariacean gastropods that show either a definite slit-bearing selenizone or a trilineate medial banding pattern. It may be that Ulrich's *L. robusta* group, characterized by shells with short rotund whorls, distinctly trilineate medial bands, growth lines and lunulae indicating a wide sinus and slit, is Foerste's *Ruedemannia,* but all attempts that I have made to construct even a tentative listing of species that may possibly be assigned to this genus have been unsuccessful. I have interpreted the trilineate banding pattern on the more rotund forms as some indication of a definite slit-bearing selenizone, but the value of this trilineate band as a generic character is unknown. Misidentification of these Upper Ordovician specimens as *Plethospira* or *Seelya* (Pl. 17, fig. 4) could result because the central Appalachian material shows little or no preservation of the aperture or columellar lip, but *Plethospira* and *Seelya* do not exhibit the characteristic spiral threads mid-way between the whorl periphery and sutures typical of *Ruedemannia* and *Loxoplocus* (*Lophospira*).

Ruedemannia? *lirata* is found only in north-central Pennsylvania, gastropod faunal province I (loc. 34-A, 50) at the northern limits of the pleurotomariacean distribution (Fig. 16). It is never a dominant faunal element but is locally common. The associated faunal elements are crinoids, *Hallopora* and *Ctenodonta*? *pulchella,* part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. Bassler (1919, p. 296) noted fragments of *L.* (*Ruedemannia*) *lirata* in the sandstone debris of the upper part of the Martinsburg Formation in Washington County, Maryland. I was unable to confirm this find, although my locality 124, in the same area, did produce characteristically abundant crinoids and trepostomatous bryozoans.

The substratum is composed of muddy silts, never reworked, finely laminated although occasionally showing shale pebble fragments. An inner or outer sublittoral, quiet water environmental setting appears to be indicated by the associated fauna, substratum type, geographic and stratigraphic position. *R.*? *lirata,* like all other Pleurotomariacea, probably required a firm substratum, non-turbid waters, and fed on macrophagous plant detritus.

Only one other gastropod occupies the northernmost portions of the Reedsville exposures, and less than ten specimens were found, all of which occur within gastro-

pod faunal province I (Fig. 16). It is *Cyclonema* (loc. 75; Pl. 17, fig. 5), a platyceratacean with life habits probably quite distinct from those of *R.? lirata*, although these two species occasionally are associated with similar faunal elements; *Cyclonema* normally is found with crinoids, *Lyrodesma poststriatum*, *Ambonychia radiata* and *Rafinesquina "alternata"*, part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. It is thought that the Upper Ordovician *Cyclonema*, like the Devonian species of *Cyclonema*, may have been coprophagous commensals on crinoids (Bowsher, 1955).

Subfamily LOPHOSPIRINAE
Genus *LOXOPLOCUS*

Loxoplocus (*Lophospira*) *abbreviata* (Hall, 1847)
Plate 18, figures 4-6

Murchisonia uniangulata var. *abbreviata* Hall, 1847, p. 304, pl. 83, fig. 2d; [?]2a, 2b, 2c.

[?]*Schizolopha moorei* Ulrich (*in* Ulrich and Scofield), 1897, p. 992, pl. 65, figs. 31-37.

Lophospira uniangulata var. *abbreviata* (Hall). Whitfield and Hovey, 1898, p. 52.

[?]*Ruedemannia abbreviata* (Hall). Foerste, 1914a, p. 311.

Lophospira abbreviata (Hall). Ruedemann, 1926, p. 65, pl. 8, figs. 11, 13, [?]12.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size (median height of 12 specimens, 7 mm), conispiral, high spired. Whorl profile slope about 25 degrees from vertical; whorl surface broadly rounded, slight angulation near suture, no pronounced spiral threads. Aperture unknown. Umbilicus unknown. Sutures sharp, deep. Spiral band at whorl periphery raised, angular; lunulae unknown. Surface sculpture fine, faintly preserved as external molds, intersection with peripheral spiral band broadly angular, not sharp or swept backwards. All internal features unknown. Shell mineralogy and microstructure unknown.

Materials. The description is based on about 40 specimens from north-central Pennsylvania and northern Virginia deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Loxoplocus* (*Lophospira*) *abbreviata* is tentative. A problem of assignment arises from the subsequent designation of lectotypes by Foerste (1914a) and Ruedemann (1926) from Hall's *Murchisonia uniangulata* var. *abbreviata* material (1847, pl. 83, figs. 2a-2d). Foerste (1914a, p. 311), reworking Hall's material, formally designated Hall's figure 2c as the lectotype of the species *Ruedemannia abbreviata*. His main criterion was that this figure showed the best developed trilineate peripheral bands and an overall sub-rotund whorl profile. However, later Foerste (1924, p. 211) failed to mention *R. abbreviata* in his vague re-definition of the genus *Ruedemannia*. The generic problems are further reviewed under the discussion of *R.? lirata* (see p. 104).

Ruedemann (1926), working in western New York, uncovered abundant specimens from the upper part of the Whetstone Gulf and lower Pulaski Formations, pos-

sibly topotypic with Hall's *Murchisonia uniangulata* var. *abbreviata,* and designated them as *Lophospira abbreviata.* Ruedemann (1926, p. 66–67) disregarded the term *Ruedemannia* and Foerste's formal designation of Hall's figure 2c (1847, pl. 83) as the type and instead informally designated figures 2a or 2b as the lectotype(s) of the species *L. abbreviata*, failed to mention figure 2c, and claimed that figure 2d "probably does not belong here".

It is certainly possible that Hall's syntypes do contain two distinct taxa. Hall's figure 2c appears more closely related to *R.? lirata*, and, in fact, Ruedemann's figure 12 (1926, pl. 8), a fragment of an apparently non-related exterior, showing a definite selenizone with broadly concave lunulae and growth lines sweeping well back along the flanges of the selenizone, also resembles *R.? lirata.* The central Appalachian Upper Ordovician specimens correspond more closely to Hall's figure 2d (1847, pl. 83) and Ruedemann's figures 11 and 13 (1926, pl. 8). They appear to be non-slit-bearing forms and, although broadly rounded, they do not resemble *R.? lirata. L.* (*L.*) *abbreviata* must be classified as *nomen inquirendum* pending a complete taxonomic review of this material.

Loxoplocus (*Lophospira*) *abbreviata* is common at localities in south-central Pennsylvania (see Table 3, loc. 101, 106, 107) and in central Virginia (loc. 167, 169, 172; see Fig. 16) always along the eastern edge of the Reedsville exposures, gastropod faunal province I. Rare specimens of *L.* (*L.*) *abbreviata* have also been identified to the south and west of these exposures (see loc. 87, 97, 147, 148, 152, 203). The associated faunal elements usually found with *L.* (*L.*) *abbreviata* are *L.* (*L.*) *ventricosta, L.* (*L.*) *perangulata, Sinuopea*? and lesser numbers of *R.* "*alternata*", *O. linneyi* and *Modiolopsis modiolaris,* which are generally considered part of the *Sowerbyella–Onniella* Community, but rock samples include occasional species more characteristic of the Rhynchonellid Population of the *Orthorhynchula–Ambonychia* Community. I have found that specimens of *L.* (*L.*) *abbreviata* are also commonly clumped together. Ruedemann (1926, p. 66) identified *L.* (*L.*) *abbreviata* at only three localities in western New York. He considered it a rare Lorraine fossil, but occasionally very abundant locally near the contact between the Whetstone Gulf Shale and the Pulaski Formation.

The probable environmental setting of *L.* (*L.*) *abbreviata* can only be inferred from the ecology of Recent pleurotomariacean gastropods. Pleurotomariacean anatomy has been studied in detail by Yonge (1947), and in the process he has gathered a small but valuable amount of ecological data. Because these Archaeogastropoda have simple aspidobranch, bipectinate ctenidia, the animal has difficulty in freeing mud-size particles from the gill filaments. The gill structure dictates life on a firm substratum where there is little turbid water. Pleurotomariaceans are commonly macrophagous herbivores that browse on algae or move along the substratum ingesting detrital plant material (Graham, 1955, p. 149). Batten (1958, p. 169) noted that Recent Pleurotomariacea live between 50 and 200 fathoms and seem better adapted to colder, possibly deeper waters, though some can tolerate brackish water conditions.

The Upper Ordovician Pleurotomariacea are not widespread but probably occupied an inner sublittoral, quiet water environment. One of the factors controlling the distribution was probably substratum type, which, in the central Appalachians, is usually a fine, possibly firm silt or sand. The patchiness and local clumping of this gastropod may be associated with the probable irregular distribution of detrital plant

material by currents moving over the substratum. The influence of water temperature and salinity is difficult to ascertain for any of the Upper Ordovician pleurotomariacean species.

Loxoplocus (*Lophospira*) *ventricosta* (Hall, 1847)
Plate 18, figure 3

Murchisonia ventricosta Hall, 1847, p. 41, pl. 10, fig. 3. Emmons, 1855, p. 162. [not] Salter, 1859, p. 23, pl. 5, figs. 2, 2a, 3.

[?]*Lophospira peracuta* Ulrich and Scofield, 1897, p. 976, pl. 73, figs. 15-17. Wilson, 1951, p. 36, pl. 3, fig. 4.

Lophospira ventricosta (Hall). Bassler, 1915, p. 766. Wilson, 1951, p. 39, pl. 4, figs. 23, [?]22.

[?]*Lophospira manitoulinensis* Foerste, 1924, p. 213, pl. 36, figs. 5a-d.

[?]*Lophospira liosutura* Secrist and Evitt, 1943, p. 366, fig. 12.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size (height of one specimen, 18 mm; diameter of last whorl, 13 mm), conispiral, high-spired. Whorl profile slope about 25 degrees from the vertical; whorl upper surface sharply convex, angular, lower surface gently convex, spiral threads absent. Aperture unknown. Sutures prominent, shallow. Spiral band at whorl periphery raised, angular; lunulae unknown. Surface sculpture unknown. All internal features unknown. Shell mineralogy and microstructure unknown.

Materials. The description is based on 10 partial specimens from north-central Virginia deposited in the Peabody Museum.

Discussion. Assignment of these central Appalachian Upper Ordovician specimens to *Loxoplocus* (*Lophospira*) *ventricosta* is tentative. The specimens show a prominent, raised peripheral band, a sharply convex, non-threaded upper whorl surface and pronounced sutures, all of which are characteristic of numerous Lower Paleozoic *Lophospira* species, Hall (1847, p. 41) introduced the term *Murchisonia ventricosta* for some New York specimens; this appears to be the earliest description of a North American species similar to these central Appalachian forms. Wilson (1951, p. 39) remarked that Hall's illustration of the holotype (1847, pl. 10, fig. 3) is inadequate. She figures two specimens (1951, pl. 4, figs. 22, 23) from the Ottawa area identified by Billings as *Murchisonia ventricosta*, but only tentatively assigns them to the species. *L.* (*L.*) *ventricosta* must be classified as *nomen inquirendum*.

Abundant *L.* (*L.*) *ventricosta* occur in north-central Virginia, gastropod faunal province I (Table 3, loc. 167, also Fig. 17). This is the type locality of Secrist and Evitt's *Lophospira liosutura* (1943, p. 366, fig. 12), which may be conspecific with *L.* (*L.*) *ventricosta*. Dr. Ellis Yochelson kindly made available Secrist and Evitt's type material deposited in the U.S. National Museum. We have tentatively identified their figured specimens of *Lophospira liosutura* as occurring in a porous sandstone block labeled "25.6 feet". The label probably refers to Secrist and Evitt's "80 foot horizon" of the Passage Creek section (1943, p. 362), which they state is a six-inch porous bed in which *Lophospira* is very abundant. I have re-collected from this bed which has produced abundant specimens of Sinuopeidae, some *Seelya* (Pl. 17, fig. 4) and the *L.* (*L.*) *ventricosta* (?= *Lophospira liosutura*). A re-collection and more careful restudy of the gastropods along the eastern edge of the Reedsville exposures

in south-central Pennsylvania and northern Virginia where the pleurotomariacean gastropods are most common may show *L.* (*L.*) *ventricosta* to be somewhat more widely distributed, but remaining within this restricted area of the central Appalachians. *L.* (*L.*) *ventricosta* presumably lived in much the same manner as *L.* (*L.*) *abbreviata*; that is, in a quiet water, shallow sublittoral environment.

Loxoplocus (*Lophospira*) *perangulata* (Hall, 1847)
Plate 18, figures 4 and 7

Murchisonia perangulata Hall, 1847, p. 41, pl. 10, fig. 4.
Murchisonia perangulata var. A. Hall, 1847, p. 179, pl. 38, figs. 7a, 7b.
Murchisonia bicincta var. *perangulata* (Hall). Salter, 1859, p. 19, pl. 4, fig. 7.
Lophospira perangulata (Hall). Ulrich and Scofield, 1897, p. 972, pl. 73, figs. 1-3, 5-7, [?]4. Ruedemann, 1901, p. 31. Bassler, 1909, pl. 3, figs. 9-13. Wilson, 1951, p. 37, pl. 4, fig. 13.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size (median height of four specimens, 7 mm), conispiral, fusiform. Whorl profile slope about 20 degrees from the vertical; whorl surface broadly rounded, no pronounced spiral threads. Aperture unknown. Umbilicus unknown. Sutures prominent. Spiral band at whorl periphery raised, rounded, preserved as internal mold, lunulae unknown. Surface sculpture unknown. All internal features unknown. Shell mineralogy and microstructure unknown.

Materials. The description is based on about 10 mostly fragmentary specimens from central Virginia deposited in the Peabody Museum.

Discussion. The assignment of these specimens to *Loxoplocus* (*Lophospira*) *perangulata* is tentative. Hall (1847, p. 41, 179) introduced the terms *Murchisonia perangulata* for specimens found in the New York Birdseye (Lowville) Limestone, and *M. perangulata* var. A for specimens in the New York Trenton Limestone. Hall believed the Trenton variety closely resembled *M. bicincta*, with which it occurred; but he felt that further study would show it to be similar to the Birdseye *M. perangulata*.

Salter (1859, p. 19) informally placed Hall's Birdseye *M. perangulata* in synonymy with *M. bicincta*, stating that it did not differ significantly from small *M. bicincta*. Salter figured one specimen called *M. bicincta* var. *perangulata* (1859, pl. 4, fig. 7), apparently as a representative juvenile form of *M. bicincta*. The New York Trenton Limestone *M. perangulata* var. A was considered by Salter a distinct, more elongate species.

Ulrich's subsequent designation of the type *Lophospira perangulata* (in Ulrich and Scofield, 1897, p. 972) was specifically restricted to Hall's *M. perangulata*. Ulrich also considered Hall's *M. perangulata* var. A a separate species, but he designated no specific assignment and presented no synonymy. Ruedemann (1901, p. 31), working in the Trenton conglomerate of eastern New York, described specimens which he felt came nearer to Hall's Birdseye *M. perangulata* than his Trenton *M. perangulata* var. A; therefore, he justified the use of the term *Lophospira perangulata* after Ulrich.

The specimens I have collected from the central Appalachian Upper Ordovician appear in closer agreement with Hall's Trenton *M. perangulata* var. A, but I have

used the term *L.* (*L.*) *perangulata* realizing that a complete revision of this taxon is required. The following list may contain some junior subjective synonyms:

Loxoplocus (*Lophospira*) *milleri* [= *L.* (*L.*) *bicincta* (Miller)]
L. (*L.*) *medialis* (Ulrich and Scofield)
L. (*L.*) *perangulata* (Hall)
L. (*L.*) *perangulata* var. A (Hall)
L. (*L.*) *helicteres* (Salter)

Abundant specimens of *L.* (*L.*) *perangulata* occur in central Virginia (loc. 174, 177, 179), along the eastern edge of the Reedsville exposures. Specimens are rarely found outside this area. The commonly associated abundant faunal elements are *Lingula*?, *Bucania* sp., *Ischyrodonta*? *truncata* and *L.* (*L.*) *abbreviata*. The substratum is a fine silt and the most probable environmental setting is a quiet water, inner sublittoral environment. The common pattern of clustering is observed as in the other gastropods and again could be associated with the availability of food on the substratum. Recent pleurotomariacean ecology is reviewed under the discussion of *L.* (*L.*) *abbreviata* (p. 106).

Family SINUOPEIDAE
Subfamily SINUOPEINAE

Genus *SINUOPEA*?
Plate 19, figures 1-2

The identification of these central Appalachian Upper Ordovician specimens was critically reviewed by Dr. Ellis Yochelson, who believes that these pleurotomariacean gastropods can be classified only as members of the Family Sinuopeidae and do not resemble any existing genus in that family. The central Appalachian specimens are only suggestive of the genus *Sinuopea* in their deep sutures and "U" shaped sinus, and because of the pronounced shoulder of the upper whorl surface of the central Appalachian specimens the present generic assignment is in doubt.

The sinuopeid gastropods constitute an abundant faunal element only in south-central Pennsylvania and northern Virginia, gastropod faunal province I (loc. 101, 163, 167, see Fig. 16), along the eastern edge of the Reedsville exposures. The geographic distribution is close to that of *Loxoplocus* (*Lophospira*) *abbreviata* and *L.* (*L.*) *ventricosta*, faunas common to the Strophomenid Population of the *Sowerbyella–Onniella* Community. Other less common associated faunal elements are *Trochonema* (Pl. 17, fig. 6), *Maclurites*?, *Bucania* sp., *Ischyrodonta truncata* and *Orthorhynchula linneyi*. A few sinuopeids are also occasionally found with *Tancrediopsis cuneata*, *Lingula*?, *Plectonotus*? sp. (loc. 84), i.e., the Linguloid Population of the *Orthorhynchula–Ambonychia* Community, and the crinoids, *Onniella multisecta* and *Sowerbyella* (*Sowerbyella*) *sericea* (loc. 107), part of the Strophomenid Population of *Sowerbyella–Onniella* Community. The two latter faunal associations are found to the west and north of the main pleurotomariacean belt in south-central Pennsylvania, gastropod faunal province I (Fig. 16).

The patchiness of the sinuopeid gastropod distribution seems to be characteristic of all Upper Ordovician pleurotomariaceans. The sinuopeid occurrences define a

broadly linear north-south belt from south-central Pennsylvania to northern Virginia. The environmental setting of the pleurotomariid gastropods is reviewed under the discussion of *L.* (*L.*) *abbreviata*, p. 106. The sinuopeids are believed to have differed little from the other Pleurotomariacea in their life habits.

?Suborder MURCHISONIIA
Superfamily MURCHISONIACEA
Family MURCHISONIIDAE

Genus *MURCHISONIA*?

Plate 19, figures 3-4

The assignment of these Upper Ordovician specimens was reviewed by Dr. Ellis Yochelson, who felt that the quality of preservation permitted classification only as representative of the Family Murchisoniidae. The infrequent, but well-defined, peripheral band, the fusiform whorl profile, and the deep sutures are somewhat reminiscent of the genus *Murchisonia*, but again the generic assignment is in doubt.

The murchisoniid gastropods are found only along Clinch and Cumberland Mountains in northern Tennessee, gastropod faunal province III (loc. 130, 133, 135; see Fig. 16). The rock type is consistently a silty mud or carbonate mud, in direct contrast to the silt-fine sand substratum associated with the bellerophontid and pleurotomariid gastropods. The taxonomic diversity of the murchisoniid faunal association is notably lower than in the other two gastropods; *Zygospira recurvirostra* from the Spiriferid Population of the *Zygospira–Hebertella* Community is the only abundant associated faunal element, although a few *Pterinea* (*Caritodens*) *demissa* and large *Loxoplocus* (*Lophospira*) sp. are present with the murchisoniids.

Cox and Knight (1960, p. I290) reviewed the taxonomic status of the Superfamily Murchisoniacea and thought it could be considered an archaeogastropod, a mesogastropod, or a transitional form between the two. The submedial sinus and slit, presumably exhalant in function, point to the Pleurotomariina (Archaeogastropoda), whereas the high-spired, many-whorled nature of the murchisoniids and their tendency to develop what appears to be an inhalant channel suggests a Cerithiacea (mesogastropod) stock. The suborder Murchisoniina was erected by Cox and Knight (1960) for the reception of the Superfamily Murchisoniacea, in the belief that the murchisoniids still retain the primitive features of the Archaeogastropoda but show some characteristic evolutionary advances along the lines leading to the Mesogastropoda.

The morphologically transitional nature of the murchisoniids may be reflected in their Upper Ordovician environmental setting that places them geographically apart from the abundant Archaeogastropoda (Bellerophontacea and Pleurotomariacea). Yonge (1947, p. 495) noted that the complex bipectinate aspidobranch ctenidium of the Archaeogastropoda is easily fouled by sediment, and mud particles can be removed from the ctenidia only with difficulty. Therefore, Recent pleurotomariid gastropods as a whole can exist effectively only in clear waters and on a firm substratum. As Lower Paleozoic pleurotomariid populations probably expanded gradually into muddier substrata, those individuals possessing a ctenidial structure from which mud particles could be more easily removed would have had a selective advantage. Along with the development of the monopectinate ctenidium, evolutionary changes advantageous to the mud-dwellers would be the emergence of an extensible inhalant

siphon and modification of the foot to allow the ancestral mesogastropod to move on or through a soft substratum.

BIVALVIA
Plates 20-44

The Bivalvia, next to the Brachiopoda, are the most abundant and widespread faunal element in the central Appalachian Upper Ordovician rocks. The class is represented by five superfamilies and ten common species. There are rare and scattered specimens of two additional superfamilies, Nuculanacea (*Nuculites* and *Palaeoneilo*) and Cyrtodontacea (*Cyrtodonta*?).

The taxonomy and systematics of the North American Ordovician Bivalvia have been neglected for over half a century, but recent studies of Lower Paleozoic nuculoids by McAlester (1963, 1964, 1968) and ambonychiids by Pojeta (1962, 1966) mark the beginning of renewed interest. Investigations of European species by Isberg (1934) and the excellent survey by Babin (1966) have been of considerable use in this study. Papers dealing with the Ordovician Bivalvia of eastern North America include Hall (1847), Hall and Whitfield (1875), Ulrich (1893, 1894), Bassler (1919), Stewart (1920), Foerste (1924), Ruedemann (1926) and Wilson (1956).

Phylum MOLLUSCA
Class BIVALVIA
Subclass PALAEOTAXODONTA
Order NUCULOIDA
Superfamily CTENODONTACEA
Family CTENODONTIDAE
Genus *CTENODONTA*?

Ctenodonta? *pulchella* (Hall, 1847)
Plate 20, figures 1-4

Lyrodesma pulchella Hall, 1847, p. 302, pl. 82, figs. 12a, b, d; [not]12c.
Leda pulchella (Hall). Emmons, 1855, p. 173.
Tellinomya (*Lyrodesma*) *pulchella* (Hall). Hall, 1856, p. 395. Hall, 1857c, p. 136.
Ctenodonta pulchella (Hall). Ulrich, 1894, p. 581. Foerste, 1914, p. 305. Ruedemann, 1926, p. 14.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size, broadly oval, equilateral (median height of five specimens, 7 mm; median length, 7 mm). Shape variation appears limited to very slight differences in height-length properties. Surface sculpture of fine concentric striae. Taxodont teeth of moderate size, decreasing in size toward the umbo; teeth continuous beneath umbo. Resilifer absent, ligament area otherwise unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on about 20 specimens from north-central Pennsylvania deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician speci-

mens to the genus *Ctenodonta* is tentative, pending a thorough restudy of all Upper Ordovician nuculoid bivalves. Until recently all North American Ordovician nuculoid bivalves had been assigned to the genus *Ctenodonta*, but many of these species do not appear to be congeneric with the type *Ctenodonta nasuta* (McAlester, 1963). This is true for *Ctenodonta? pulchella*, which I believe may merit a separate generic designation after a restudy of other North American material, and hence the present generic assignment is questioned.

Ulrich (1894, p. 581) placed *C. pulchella* in his Group IV, ctenodonts typified by *C. pectunculoides*. Group IV consisted of five species:

Ctenodonta pulchella (Hall, 1847)
C. pectunculoides (Hall, 1871)
C. cingulata (Ulrich, 1879)
C. subrotunda (Ulrich, 1892)
C. circularis Ulrich 1894

The first three appear to form an internally coherent morphological grouping, but *C. subrotunda* may be a *Palaeoconcha* Miller, 1889 and *C. circularis* is a *nomen nudum*, as the species was never described or figured. The following is my tentative listing of possible congeneric species. No evaluation of the subjective synonymies that may exist in this list is possible at the present time.

Ctenodonta pulchella (Hall, 1847)
C. pectunculoides (Hall, 1871)
C. cingulata (Ulrich, 1879)
C. lorrainensis Foerste 1941
C. borealis Foerste 1924

Ctenodonta? pulchella is abundant at localities 34-A, 35, and 37 in north-central Pennsylvania, bivalve faunal province I, and is very rarely found outside this area (Fig. 17). Associated faunal elements include *Praenucula levata, Lyrodesma poststriatum*, crinoids and occasionally *Hallopora, Zygospira modesta* and *Onniella multisecta*, part of the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community. The substratum is commonly a finely laminated silt and mud; the environmental setting appears to have been sublittoral and subjected to only moderate turbulence. By analogy with Recent nuculoid bivalves, *C.? pulchella* was probably an infaunal detritus feeding form, a life habit that is locally dominant in these Upper Ordovician offshore mud and silt environments.

Genus *TANCREDIOPSIS*

Tancrediopsis cuneata (Hall, 1856)

Plate 21, figures 1-7; plate 22, figures 1-6; plate 23, figures 1-5; plate 24, figures 1-3

Tellinomya cuneata Hall, 1856, p. 392, figs. 6, 7. Hall, 1857a, p. 183, figs. 6, 7. Hall, 1857b, p. 143, figs. 6, 7. [not] Hall, 1862b, p. 38, figs. 1, 2.

Ctenodonta contracta Salter, 1859, p. 37, pl. 8, figs. 4, 5. Logan, 1863, p. 175, figs. 160a, b. Wilson, 1956, p. 23, pl. 2, figs. 7-9.

Ctenodonta (Tancrediopsis) contracta (Salter). Beushausen, 1859, p. 70.
[?]*Tellinomya contracta*? (Salter). Walcott, 1884, p. 76, pl. 11, figs. 15, 15a.
Tancrediopsis cuneata (Hall). McAlester, 1963, p. 5, figs. 1-80.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size, equivalved, strongly inflated, umbones very prominent (median length of 42 specimens, 14 mm; median height, 9 mm). Shape variable, height ranging from 57 to 76 per cent of length (median of 42 measured specimens, 66 per cent). Surface sculpture of faint, widely spaced concentric striae; sculpture usually obscure because of internal mold preservation. Large, chevron-shaped taxodont teeth; about equal numbers of teeth on either side of, and pointed toward, umbo; teeth are continuous beneath umbo but decrease in size. Resilifer absent, ligament area otherwise unknown. Anterior and posterior adductor muscle scars prominent, emphasized by sharp ridge on inner side of each scar, more prominent on anterior; pedal retractor muscle scars small but prominent, located at dorsal end of the inner adductor ridges; other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on over 200 specimens from central Pennsylvania to southeastern Virginia deposited in the Peabody Museum.

Discussion. The taxonomic status of *Tancrediopsis cuneata* was reviewed by McAlester (1963). My central Appalachian specimens can be assigned to this species and exhibit only slight morphological variation from northern to southern localities, bivalve faunal province II (Fig. 17). They remain constantly associated with the same abundant faunal elements, *Lingula*?, *Plectonotus*? sp. and occasionally *Ischyrodonta truncata*, part of the Linguloid Population of the *Orthorhynchula–Ambonychia* Community. This faunal assemblage dominates inner sublittoral and intertidal environments from central Pennsylvania into central Virginia and is apparently able to tolerate variations in substratum (muddy silts to medium sand), possibly salinity, and temperature. A more complete review of the ecological requirements of this assemblage is presented in the chapter on paleoautecology (p. 36).

Not included in this description are some questionable nuculoid bivalves from localities 135 and 148 in southwestern Virginia and Tennessee, bivalve faunal Province III (Pl. 20, figs. 9-11). They may belong to the genus *Palaeoneilo* Hall and Whitfield, 1869, although their poor preservation does not permit any positive assignment; only the notable posterior expansion gives any clue to the taxonomic placement of these specimens. They are smaller than the typical *T. cuneata* (median length of 23 specimens, 11 mm; median height, 5 mm) and are found almost to the exclusion of any other faunal elements at localities 135 and 148, but the species may be part of the *Zygospira–Hebertella* Community.

Superfamily NUCULACEA
Family PRAENUCULIDAE
Genus *PRAENUCULA*

Praenucula levata (Hall, 1847)
Plate 20, figures 5-8

Nucula levata Hall, 1847, p. 150, pl. 34, figs. 1a-d, f-i; [?]1e, k.

Leda levata (Hall). Emmons, 1855, p. 137, pl. 14, fig. 10.
Tellinomya (*Nucula*) *levata* (Hall). Hall, 1856, p. 395. Hall, 1857c, p. 136.
Ctenodonta levata (Hall). Billings, 1863, p. 175, figs. 161a, b. Ruedemann, 1912, p. 100, pl. 6, fig. 1. Wilson, 1956, p. 25, pl. 2, figs. 10-13.
Tellinomya levata (Hall). Hall, 1871, pl. 3, fig. 27. Hall, 1872, pl. 7, fig. 27. Hall and Whitfield, 1875, p. 82, pl. 1, fig. 23.
[?]*Ctenodonta filistriata* (Hall and Whitfield). Ulrich, 1894, p. 599, figs. 44a-e. Bassler, 1919, p. 297, p. 54, figs. 26-29. [?]Stewart, 1920, p. 9, pl. 1, fig. 5. Foerste, 1924, p. 134, pl. 18, figs. 7a, b. Ruedemann, 1926, p. 14, pl. 1, figs. 13, 14.
Tellinomya (*Ctenodonta*) *levata* (Hall). Clarke and Ruedemann, 1903, p. 521.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small size, equivalved, anteriorly elongated (median length of eight specimens, 7 mm; median height, 5 mm). Shape variable, height ranging from 62 to 84 per cent of length (median of eight measured specimens, 78 per cent); distance from anterior extremity to umbo ranging between 57 and 64 per cent of length (median of six measured specimens, 62 per cent). Surface sculpture unknown, preserved only as internal molds. Prominent taxodont teeth, chevron-shaped, pointed toward umbo; teeth continuous but decreased abruptly in size under umbo; subequal in size on either side of umbo. Resilifer absent, ligament area otherwise unknown. Anterior muscle scar subround, weakly impressed; other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on about 10 specimens from central Pennsylvania deposited in the Peabody Museum.

Discussion. A survey of the North American Ordovician literature reveals that some species now assigned to the genus *Ctenodonta* probably belong to the genus *Praenucula* Pfab, 1934. I have tentatively assigned my central Appalachian specimens to this genus pending taxonomic re-evaluation of other North American material.

Hall (1847, p. 150) remarked in his description of *Ctenodonta* (= *Nucula*) *levata* that the shell "presents considerable variation in form, even in the same locality." But it appears that his figures show more than one species; i.e., figures 1e and 1k (pl. 34) appear to belong to the genus *Palaeoconcha* Miller, 1889. The other figures seem to be *Praenucula*, although they show considerable variation in the degree of posterior expansion. Hall designated no type for the species *C. levata*. Wilson (1956, p. 25) also has noted that Hall's material appeared to contain more than one species, but she stated that Ulrich and Ruedemann after examination of Hall's specimens decided upon a lectotype for *C. levata*. Wilson further pointed out that the specimen chosen by Ulrich and Ruedemann was figured by Ruedemann (1912, pl. 6, fig. 1), but I have found no subsequent type designation presented by Ruedemann (see 1912, p. 110). Furthermore there is no discussion of the status of Hall's syntypes by either Ruedemann or Wilson. That plate 6, figure 1 (Ruedemann, 1912) is the subsequently designated type of *C. levata* rests on the interpretation of Wilson (1956). No authors have considered the difficulties created by the shape variation that Hall's specimens show, or faced the obvious problems of preservation that appear to have plagued Wilson (1956, p. 25). What appears to me to have been the supposed "key criterion" for the identification of *C. levata*, the slightly subangular anterodorsal projection, is rarely preserved.

McAlester (1968, p. 46) described the type species of the genus *Praenucula* (*Praenucula expansa* Pfab, 1934) as being of unknown shape variability, although showing a well-defined anterior elongation. I have listed below the North American species that may belong in this genus; there are notable differences in the degree of anterior expansion, but all appear to show subequally sized taxodont teeth on either side of the umbo.

Ctenodonta levata (Hall, 1847)
C. donaciformis (Hall, 1847)
C. abrupta Billings 1865
C. nitida (Ulrich, 1892)
C. medialis Ulrich 1894
C. scofieldi Ulrich 1894
C. retrosa Ulrich 1893 (1895)
C. filistriata Ulrich 1894
C. albertina Ulrich 1894
C. simulatrix Ulrich 1894
C. madisonensis Ulrich 1894
C. calvini Ulrich 1894
C. perminuta Ulrich 1893 (1895)
C. nuculiformis (Hall, 1847)
C. (?) *hilli* (Miller, 1874)
[?]*C. socialis* Ulrich 1894
[?]C. *fecunda* (Hall, 1862)

This group includes most of Ulrich's *C. levata* or Group III ctenodonts (1894). Excluded are:

Ctenodonta hartsvillensis Safford 1869, probably a *Palaeoconcha*
C. danvillensis Ulrich 1894, *nomen nudum*
C. tumida Ulrich 1894, *nomen nudum*
C. mundula Ulrich 1894, *nomen nudum*

Those species designated as *nomina nuda* have never been figured or described. Additions to the list of possible North American *Praenucula* include the following:

Ctenodonta planodorsata (Ulrich, 1892)
C. prosseri Ruedemann 1912
C. radiata Ruedemann 1912
C. recta Ruedemann 1912
C. myalta Stewart 1920
C. chambliensis Foerste 1924
C. hyacinthensis Foerste 1924

Praenucula levata is commonly found with *C.? pulchella, Lyrodesma poststriatum* and lesser numbers of crinoids, *Hallopora* and *Onniella multisecta*, which are part of

the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community, at localities 37, 52, and 97 in central Pennsylvania, bivalve faunal province I (Fig. 17). Ruedemann (1926, p. 15) also found what appear to be species of *Praenucula* and *Ctenodonta*? commonly associated throughout the Whetstone Gulf Shale in western New York. The environmental setting for the central Appalachian species appears to be in quiet, offshore waters. The substratum is a finely laminated silt and mud which is dominated by small patches of infaunal, detritus feeding nuculoid bivalves. *P. levata* and *C.? pulchella* constitute the greatest number of these infaunal forms, although there are scattered specimens of *Nuculites* and *Palaeoconcha*.

Subclass PTERIOMORPHIA
Order PTERIOIDA
Suborder PTERIINA
Superfamily AMBONYCHIACEA
Family AMBONYCHIIDAE
Genus *AMBONYCHIA*

Ambonychia radiata Hall 1847
Plate 36, figures 1-6

Pterinea carinata Emmons, 1842, p. 204, fig. 111.1. Vanuxem, 1842, p. 64, fig. 9.1. Owen, 1844, p. 376. Emmons, 1855, p. 175, pl. 17, fig. 23.

Ambonychia radiata Hall, 1847, p. 292, pl. 80, figs. 4a, b, c, f, [not]figs. 4d, h-l. Hall, 1859a, p. 8; p. 110, figs. 1, 2. Hall, 1859b, p. 269; p. 523, figs. 1, 2. Hall, 1862b, p. 54, figs. 11.1, 11.2. [not]Billings, 1863, p. 215, fig. 219. Hall and Whitfield, 1875, p. 79, pl. 2, fig. 2. Stoliczka, 1870, p. XXI. Stoliczka, 1871, p. 387.

Ambonychia carinata (Emmons). Lesley, 1889, p. 22, fig. 111.b.

Byssonychia radiata (Hall). Ulrich, 1893 (1895), p. 629. Foerste 1914a, p. 273, pl. 3, figs. 12A-C. Bassler, 1919, p. 282, pl. 57, fig. 26. Stewart, 1920, p. 23, pl. 4, fig. 3. Foerste, 1924, p. 164, pl. 27, figs. 3a, b; pl. 31, figs. 13a, b, c. Ruedemann, 1926, p. 27, pl. 3, figs. 4-7. [not]Butts, 1941, p. 127, pl. 100, figs. 6-8. [not]Wilson, 1948, p. 144, pl. 18, fig. 16. Pojeta, 1962, p. 183, pl. 22, figs. 1-15; pl. 23, figs. 1-14; pl. 24, figs. 1-7.

Byssonychia vera Ulrich, 1893 (1895), p. 629, figs. a-c. Bassler, 1919, p. 282, pl. 54, figs. 34-36. Stewart, 1920, p. 25, pl. 1, figs. 23, 24. [not]Butts, 1941, p. 127, pl. 100, fig. 9.

Byssonychia bowmani Secrist and Evitt, 1943, p. 363, figs. 4, 5.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of small to medium size, moderately inflated, equivalved, rounded posterior expansion (median diagonal of six specimens, 24 mm; median length, 20 mm). Shape only slightly variable, length varying between 82 and 85 per cent of the diagonal. Byssal gap prominent, elliptical, small; byssal sinus moderate. Anterior margin rounded; umbones rounded. Surface sculpture of radial ribs, about 50; faint concentric striae. Small cardinal teeth, one or two, radiating from beneath umbo; posterior lateral teeth, two or three, elongate. Ligament longitudinally striated, ligament area otherwise unknown. Posterior adductor large, subround; other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on over 15 specimens from central Pennsylvania deposited in the Peabody Museum.

Discussion. Pojeta (1962, p. 183; 1966, p. 172) discussed in detail the taxonomic status of this species, the type of the genus *Ambonychia*. The Upper Ordovician Appalachian specimens that I have assigned to this species are abundant at some locales (loc. 72, 78), and are confined geographically to central Pennsylvania, bivalve faunal province I. Localities farther south produce some questionable *A. radiata* fragments, though the ribbing appears to resemble *A. ulrichi* (esp. loc. 127). I recollected from Secrist and Evitt's (1943) type locality of *Byssonychia bowmani* (my locality 167) and found most specimens indistinguishable from *A. radiata*; there were a few specimens that appear similar to *A. praecursa* but are too poorly preserved for an accurate identification.

Almost all of the North American literature seems to emphasize the importance of *A. radiata* as the characteristic *Ambonychia* in the central Appalachians, but this is certainly not the case, as *A. praecursa* is far superior in numbers. I believe that the misidentification of *A. praecursa* as *A. radiata* has accounted for much of the discrepancy. The variability of shell shape recorded by me must be viewed cautiously because there are few whole *A. radiata* in the central Appalachian collection. My central Appalachian *A. radiata* are, however, slightly smaller and more rounded than are most previously figured specimens.

A tentative listing of possible subjective synonyms of *A. radiata* includes the following:

Ambonychia obesa (Ulrich, 1893)
A. alveolata (Ulrich, 1893)
A. retrorsa Miller 1878
A. hyacinthensis (Foerste, 1924)

The environmental setting of *A. radiata* is treated under the discussion of *A. praecursa*. The common associated faunal elements are *Rafinesquina "alternata"*, *Sowerbyella* (*Sowerbyella*) *sericea*, *Onniella multisecta*, crinoids and occasionally *Praenucula levata* and *Ctenodonta? pulchella*, all part of the *Sowerbyella–Onniella* Community.

Ambonychia praecursa (Ulrich, 1893)

Plate 37, figures 4-5; plate 38, figures 1-2, 4-5; plate 39, figures 1-4; plate 40, figures 1-4; plate 41, figures 1-3; plate 42, figures 3-4

Byssonychia praecursa Ulrich, 1893 (1895), p. 633, pl. 45, figs. 1, 2. Bassler, 1919, p. 283, pl. 57, figs. 28, 29. Stewart, 1920, p. 24, pl. 1, fig. 27. Foerste, 1924, p. 167, pl. 28, figs. 2a, b. Ruedemann, 1926, p. 30, figs. 9, 10. Pojeta, 1962, p. 191, pl. 27, figs. 1-7.

Byssonychia walkerensis Grabau, 1913, p. 454.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size, strongly inflated, equivalved, broad posteroventral elongation (median diagonal of 234 specimens, 38 mm; median length, 25 mm).

Shape variable, length varying between 64 and 78 per cent of the diagonal (median of 234 specimens, 67 per cent). Byssal gap prominent, elliptical; byssal sinus shallow. Anterior margin almost flat, umbones not rounded. Surface sculpture of prominent radial ribs (35 to 40), some ribs bifurcating near the hinge line (Pl. 41, fig. 2); finer concentric striae, closely spaced, numerous; and prominent concentric striae, wide-spaced, very few. Cardinal teeth two, radiating from beneath umbo; lateral teeth two, short and confined to posterior end of hinge line. Ligament longitudinally striated, ligament area otherwise unknown. Internal features unknown. Original shell microstructure and mineralogy unknown.

MATERIALS. The description is based on over 1600 specimens from south-central Pennsylvania to southwestern Virginia deposited in the Peabody Museum.

DISCUSSION. The assignment of these specimens to *Ambonychia praecursa* conflicts with earlier central Appalachian reports in which assignment was made rather vaguely to *A. radiata*. A re-collection from a locality listed by Grabau (1913, my locality 140) has produced topotypes of *A. walkerensis* which are indistinguishable from *A. praecursa*.

Ulrich (1893, p. 633) in his original definition of *A.* (= *Byssonychia*) *praecursa* was unsure of its exact taxonomic status. He thought it could be either a true species or a variety of *A. richmondensis*, adding that *A. praecursa* could be the "forerunner" of *A. richmondensis*, *A. robusta* or *A. cultrata*, and was shaped like *A. radiata*. Most later authors have accepted *A. praecursa* as a true species. Unfortunately its systematic relationships to the other *Ambonychia* mentioned by Ulrich have never been discussed, and the size and shape variability that puzzled Ulrich has never been adequately defined.

In addition to *A. praecursa*, collections of *Ambonychia* specimens from central Appalachian Upper Ordovician rocks yield *A. radiata* and *A. cultrata*. An investigation of the general size-shape-variability of the three species points up a possible environmental control on distribution of the species. Medians of the diagonal and length, and the ratio of these two measurements from the central Appalachian specimens are shown in Table 19. The shell shape variations that exist among these three species of *Ambonychia* are diagrammed in Figure 32. Comparisons of shell morphology, abundant faunal associates, and substratum as determined from the central Appalachian species are shown in Table 20.

Table 20 and Figure 32 present a very simplified picture of *Ambonychia* shell morphology as it is probably related to the environmental setting. Each of the three species was most probably an epifaunal, byssally attached, mussel-like bivalve. The prominent byssal gap and equivalved form emphasize an attached upright mode of

TABLE 19. Measurements of the diagonal and length of the three common species of the genus *Ambonychia*. Of particular note is the length-diagonal ratio which is used as a general measure of shape variability and possibly related to environmental setting.

Species	Diagonal (mm)	Length (mm)	L/D (%)	N
A. praecursa	38	25	67	240
A. cultrata	51	37	78	26
A. radiata	24	20	82	12

TABLE 20. Comparisons of the morphology and abundant associated faunal elements of the genus *Ambonychia*. This table forms the basis for subsequent interpretations of central Appalachian Late Ordovician environmental setting (see also Fig. 32).

Species	*A. radiata*	*A. praecursa*	*A. cultrata*
Size	small	medium	large
Shape	subround	moderately elongate	subround
Byssal gap	small, ellipsoidal	large, ellipsoidal	large, elongate
Anterior edge	rounded	flat	flat
Dentition	weak	strong	unknown
Associated faunal elements	crinoids *Rafinesquina* *Praenucula* *Ctenodonta*?	*Modiolopsis* *Orthorhynchula* *Ischyrodonta*	*Modiolopsis* *Zygospira recurvirostra* *Pterinea* (*Caritodens*) Trepostomes
Populations	Orthid–Crinoid Population; *Sowerbyella–Onniella* Community	Modiolopsid and Rhynchonellid Populations; *Orthorhynchula–Ambonychia* Community	Spiriferid Population; *Zygospira–Hebertella* Community
Substratum	silty mud–mud	fine sand–silt	silty mud–mud

life. Pojeta (1962, p. 182) finds a Recent analogue in *Mytilus* and *Modiolus*; in overall shape, I believe, it also somewhat resembles *Pinna*. The fine sand and silt, where numerous *A. praecursa* are present, is interpreted as one of the most physically exposed environments in the central Appalachian Late Ordovician. *A. praecursa*, with its more elongate shape, broader and flatter anterior edge of attachment, and possibly more secure articulation seems the best adapted of the three to cope with such an environment.

Ambonychia praecursa grades abruptly southward into *A. cultrata*. There is an accompanying change in substratum from a fine sand-silt to mud. *Modiolopsis modiolaris* is the only faunal associate common to both species, whereas a small spiriferid brachiopod, *Zygospira recurvirostra*; a pterioid, *Pterinea* (*Cartiodens*) *demissa*; and trepostomes, part of the Spiriferid Population, *Zygospira–Hebertella* Community, are most common with *A. cultrata*. Mixtures of the two species are found at a few localities in south-central Virginia; but to the north only *A. praecursa* is found, and to the south, only *A. cultrata*. The larger, rotund shell shape and the narrow elongate byssal gap of *A. cultrata* appear better adapted to a less turbulent environment.

Ambonychia radiata is not much smaller than some *A. praecursa* but is similar to *A. cultrata* in shape (Table 19). Its rounded, small shell with a small byssal gap, is probably adapted for environments of little water movement. *A. radiata* is more common in a silty mud and mud (Table 20) that is characteristic of deposition in low-energy environments. The faunal associates and the stratigraphic and geographic distributions strengthen the interpretations of an exposed inner sublittoral setting for *A. praecursa* of the *Orthorhynchula–Ambonychia* Community, a protected inner sublittoral for *A. cultrata* of the *Zygospira–Hebertella* Community and an outer sublittoral for *A. radiata* of the *Sowerbyella–Onniella* Community.

Ruedemann (1926, p. 31) commented briefly that a slab from the New York Lorraine Group showed one *A. praecursa* with many *A. radiata*. This sort of association is common in central Pennsylvania, bivalve faunal province I, and suggests the

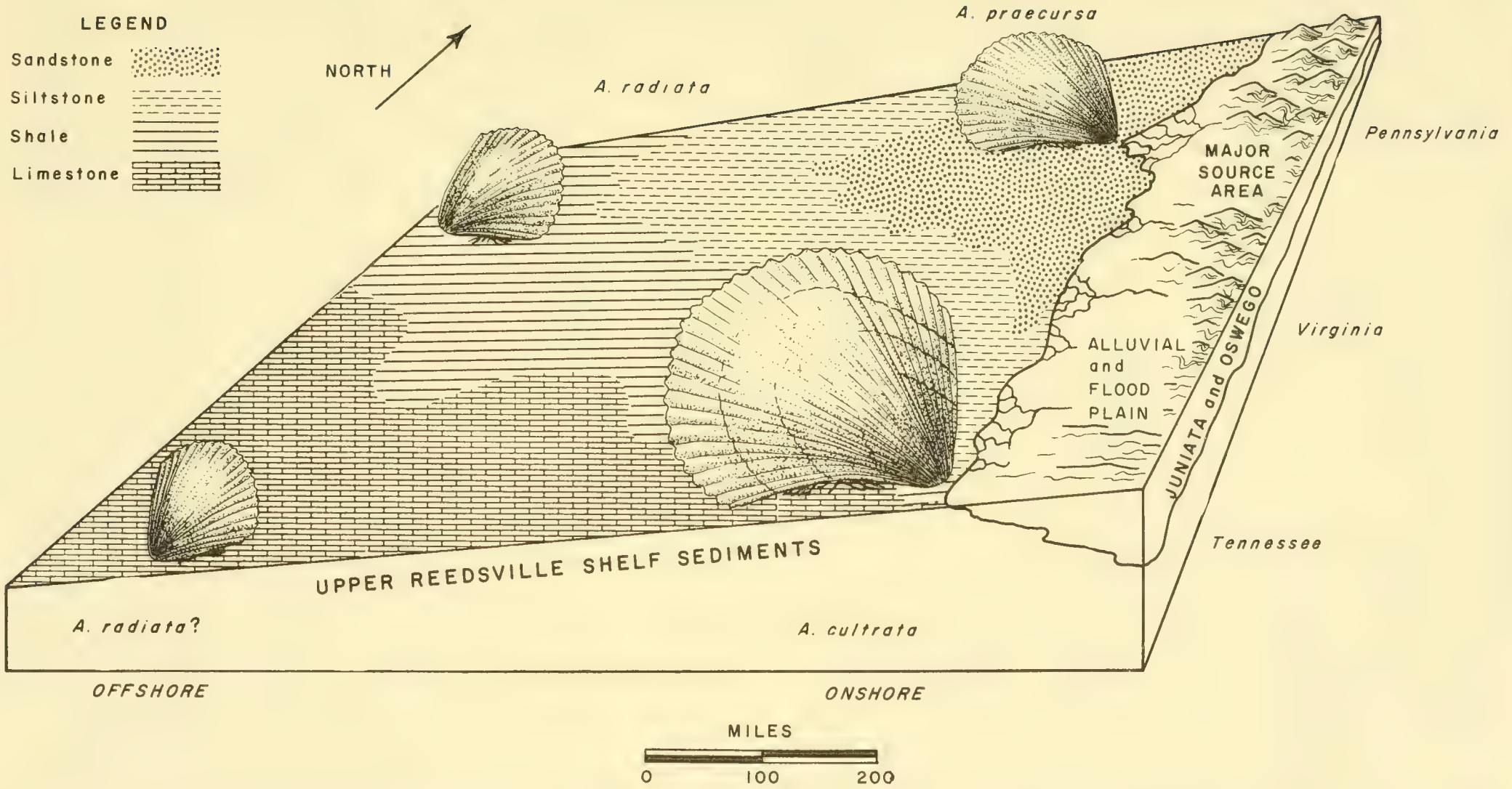


FIG. 32. Distribution of *Ambonychia* species during the Late Ordovician in the central Appalachians. Of particular note is the possibility of correlating morphological variability (i.e. general shape and size of valves) with environmental setting. Drawings of fossils are actual size of specimens. The scale refers to distance along the shore; onshore to offshore exaggeration ×4.

possibility of reworking a few dominantly inner sublittoral *A. praecursa* shells from the *Orthorhychula–Ambonychia* Community into outer sublittoral environs dominated by *A. radiata* of the *Sowerbyella–Onniella* Community. The opposite of this situation does not occur, in other words a few *A. radiata* have not been found with many *A. praecursa*, thereby possibly presenting some clue as to the relative strengths of the onshore and offshore current patterns. In fact, *A. praecursa* valves are also found within faunal assemblages dominated by numerous outer sublittoral faunal elements of the *Sowerbyella–Onniella* Community — brachiopods, crinoids and bryozoans.

Ambonychia praecursa is by far the most widely distributed *Ambonychia* in the Upper Ordovician clastic facies, bivalve faunal province II (Fig. 17). The usual faunal associates are *Modiolopsis modiolaris* and/or *O. linneyi* of the Modiolopsid and Rhynchonellid Populations of the *Orthorhynchula–Ambonychia* Community, but at three widely separated localities (Table 3, loc. 78, 152 and 203) specimens which resemble *A. praecursa*, *A.* cf. *praecursa*, are found with numerous *Tancrediopsis cuneata*, *Lingula*? and *Plectonotus*? sp., part of the Linguloid Population of the *Orthorhynchula–Ambonychia* Community. These specimens have not been included in the description of central Appalachian *A. praecursa*. Twelve specimens of *A.* cf. *praecursa* show a median diagonal of 19 mm, almost half that of the central Appalachian *A. praecursa*. From all available stratigraphic, sedimentological and paleontological evidence, species of the Linguloid Population probably dominated the nearest-shore Upper Ordovician environments. If these specimens are dwarfed *A. praecursa*, it is likely that the control may be in reduced or variable salinity (see Hallam, 1965, p. 134).

Ambonychia cultrata (Ulrich, 1893)
Plate 42, figures 1, 2; plate 43, figures 1-4

Byssonychia cultrata Ulrich, 1893 (1895), p. 632, pl. 45, figs. 5-7. Foerste, 1924, p. 166, pl. 28, fig. 6. Pojeta, 1962, p. 189, pl. 25, figs. 6-13, pl. 26, figs. 1-6.
Ambonychia cultrata (Ulrich). Pojeta, 1966, p. 174, pl. 32, figs. 1, 2.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of large size, slight to moderate inflation, broad posteroventral expansion (diagonal dimension of 15 specimens, 51 mm; median length, 39 mm). Shape variable, length varying between 74 and 81 per cent of the diagonal (median of 15 specimens, 78 per cent). Byssal gap narrow, elongate; byssal sinus moderate. Anterior margin flat, umbones not rounded. Surface sculpture of prominent radial ribs (40 to 45); less prominent fine concentric striae. Dentition unknown. Ligament broad, elongate, longitudinally striated, ligament area otherwise unknown. Internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on over 40 specimens from southwestern Virginia and northern Tennessee deposited in the Peabody Museum.

Discussion. The assignment of these specimens to the genus *Ambonychia* is tentative, for internal features and dentition are lacking. General shell shape and size suggest that this central Appalachian species is conspecific with the types of Ulrich's *Byssony-*

chia cultrata from Ohio. The environmental setting of the central Appalachian Upper Ordovician specimens of *A. cultrata* has been outlined under the discussion of *A. praecursa* (p. 119). *A. cultrata* is common only in southwestern Virginia and northern Tennessee, bivalve faunal province III (Fig. 17). The more northerly localities (Table 3, loc. 145, 147, 149, 151, 184) contains a mixture of *A. cultrata* and *A. praecursa*, but farther to the south *A. cultrata* is the dominant *Ambonychia*. It may occur entirely without *A. praecursa*, but is commonly found (loc. 131, 133, 140, 141) with a fauna dominated by *Modiolopsis modiolaris*, *Zygospira recurvirostra*, *Pterinea* (*Caritodens*) *demissa* and *Monticulipora*, from the Spiriferid Population of the *Zygospira–Hebertella* Community.

?*Ambonychia byrnesi* (Ulrich, 1893)
Plate 38, figure 3

Byssonychia(?) *byrnesi* Ulrich, 1893 (1895), p. 635, pl. 47, figs. 4, 5.
Byssonychia cf. *byrnesi* (Ulrich). Foerste, 1914b, p. 134, pl. 3, fig. 6.
Byssonychia byrnesi (Ulrich). Pojeta, 1962, p. 188, pl. 25, figs. 2-5.
Ambonychia byrnesi (Ulrich). Pojeta, 1966, p. 142, pl. 31, figs. 18-20.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size, strongly inflated, broad posterior expansion (median diagonal of three specimens, 43 mm, length one specimen, 36 mm). Shape variability unknown (length 84 per cent of diagonal in one specimen). Byssal gap small, elliptical; byssal sinus slight. Anterior margin rounded, umbones rounded. Surface sculpture of prominent radial ribs, about 25; fine concentric striae with a few widely spaced prominent concentric striae. Dentition unknown. Ligament area unknown. Shell microstructure and mineralogy unknown.

Materials. The description is based on three specimens from central Pennsylvania deposited in the Peabody Museum.

Discussion. The identification of these few specimens as *Ambonychia byrnesi* is tentative. The generic status is in doubt because no internal features are preserved, and differentiation from *A. actirostris* and *A. imbricata* is uncertain because the shell shape variation is unknown.

The specimens come from only one locality (Table 3, loc. 75) and are unlike any other *Ambonychia* in the central Appalachian Upper Ordovician strata in the strength and numbers of radial ribs. Associated with the more common *A. praecursa* in a muddy silt, near what appears to be the northern extreme of the *A. praecursa* distribution, bivalve faunal province II (Fig. 17), their general inflated shell shape, rounded appearance and small byssal gap appear to be suited to a lower energy environment than is indicated by the elongate *A. praecursa* with a large byssal gap. These specimens were not included in the simplified ecological picture presented under the discussion of *A. praecursa* because they are so few in number. *A. praecursa* in this northern environment does show some shape variability, becoming somewhat larger but no less elongate; but I am sure that these specimens called ?*A. byrnesi* could not be included within the variability limits of *A. praecursa*.

Superfamily PTERIACEA
Family PTERINEIDAE
Genus *PTERINEA*

Pterinea (*Caritodens*) *demissa* (Conrad, 1842)

Plate 24, figures 5-7; plate 25, figures 1-5; plate 26, figures 1-7; plate 27, figures 1, 2

Avicula demissa Conrad, 1842, p. 242, pl. 13, fig. 3. Emmons, 1842, p. 404, fig. 2. Hall, 1847, p. 292, pl. 80, figs. 2a, b. Emmons, 1855, p. 175, pl. 17, fig. 10.

Pterinea demissa (Conrad). McCoy, 1854, p. 260, pl. 1, fig. 7. Hall and Whitfield, 1875, p. 78, pl. 2, fig. 1. Cumings, 1908, p. 1018, pl. 48, fig. 1. Stewart, 1920, p. 22, pl. 1, fig. 28.

Pterinea (*Caritodens*) *demissa* (Conrad). Foerste, 1910, p. 71, pl. 1, fig. 10. Bassler, 1919, p. 284, pl. 57, fig. 24. Foerste, 1924, p. 161, pl. 26, fig. 3; pl. 29, fig. 10; pl. 31, fig. 12. Ruedemann, 1926, p. 23, figs. 7-11.

Caritodens demissa (Conrad). Foerste, 1914a, p. 269, pl. 1, fig. 10; pl. 3, fig. 11.

[?]*Pterinea maternata* Secrist and Evitt, 1943, p. 365, fig. 15.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size (median length of 36 specimens, 25 mm; median height of 49 specimens, 22 mm), inequivalved. Left valve convex; right valve slightly convex in umbonal region, flat to slightly concave marginally. Shape extremely variable, height ranging from 60 to 123 per cent of the length (median of 33 specimens, 94 per cent); angle formed by line drawn along the mid-part of the umbonal ridge and hinge line ranges between 55 and 75 degrees (median of 34 specimens, 65 degrees); lowest angle and obliquely prosoclinal shape most common in smaller specimens (Pl. 24, fig. 7, and Pl. 25, fig. 2); larger shells usually obtuse, rounded (Pl. 25, fig. 1, and Pl. 28, fig. 1). Byssal sinus on anterior margin, near hinge line, not pronounced. Anterior auricle and posterior wing, blunt, rounded, length of both variable. Umbones prominent, broad, rounded; posterior margin of umbonal ridge distinct, sharp subangular; anterior part broadly rounded, less prominent than posterior. Surface sculpture of two kinds of concentric striae: coarse, raised, irregular, widely spaced; and fine, regular, closely spaced. Posterior lateral tooth on left valve, corresponding socket on right valve, gently concave toward umbonal ridge, elongate; possible anterior tooth on left valve, short, projecting just beneath and anterior to umbones. Ligament duplivincular, six to eight fine longitudinal striae, amphidetic, narrow, internal. Posterior adductor large, sub-round, located centrally between ventral and dorsal margins, preserved on one right valve. All other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on over 80 specimens from West Virginia and Virginia deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Pterinea* (*Caritodens*) *demissa* is tentative, because of both the small amount of well-preserved Ordovician material upon which the taxon is defined and, especially, the lack of recent taxonomic studies of lower Paleozoic pterioids.

Foerste (1910, p. 71) established the subgenus *Caritodens* (which he later raised to generic rank) for what he believed to be a distinct Upper Ordovician pterioid that

could be distinguished from *Pterinea* by the absence of the duplivincular ligament and of well-defined multiple anterior and posterior teeth. The type, *C. demissa* (Conrad), exhibits only one strong posterior "crural" ridge, or "jugum", which culminates in a posterior lateral tooth, and also a short, blunt anterior projection. Subsequently Foerste (1914a, p. 269) discovered better preserved Ordovician material that showed a definite duplivincular ligament. Thus the definition of *Caritodens* rests solely on the presence of the single "crural" ridge.

Foerste had failed to figure *C. demissa* with the posterior "crural" ridge and the loss of the material prior to his 1924 publication makes the documentation less well-established. Ruedemann, however, figured a New York specimen (1926, pl. 2, fig. 8) that does show the characteristic posterior jugum, which I have found to be typical in all my central Appalachian Upper Ordovician material.

One of the major problems facing the earlier investigators in the definition and identification of Ordovician pterioids, aside from the characteristic poor preservation, was the extreme shape variation. The definition of a number of Ordovician species was based on slight changes in shape or minor differences in the concentric surface sculpture. The following is a list of North American Ordovician pterioid species that may be junior subjective synonyms of *P. (C.) demissa.*

Pterinea insueta (Emmons)
P. obtusiformis Ruedemann
P. cincinnatiensis Miller and Faber
P. rugatula Miller and Faber
P. prolifica Billings
P. bellilineata Billings
P. macronota Ulrich

Secrist and Evitt (1943, p. 365, fig. 15) figured a very poorly preserved specimen called *P. maternata* that was collected from their Passage Creek locality at Massanutten Mountain, north-central Virginia. I have re-collected from this locality (loc. 167) and do not feel that my material can be satisfactorily distinguished from *P. (C.) demissa.*

The problem of shell shape and its significance as a discriminator of species was the topic of lengthy discussions by Foerste (1914a, p. 269; 1924, p. 161) and of a summary statement, with illustrations, by Ruedemann (1926, p. 24-25). Without any knowledge of possible allometric growth in Recent pterioid species, Foerste introduced the idea that the younger, smaller *P. (C.) demissa* are characteristically more oblique, whereas the more mature, larger specimens are more ovate. He concluded that the direction of maximum growth along the shell edge changed drastically through time; "Small specimens appear so different from mature ones as to suggest their belonging to a different species" (Foerste, 1924, p. 161). However, Hynd (1955), working with the Recent *Pinctada albina*, an abundant pterioid found along the coastline of northern Australia, confirmed this dramatic change in shell shape with age, and found that every one of the taxonomic shape characters usually described is subject to considerable change.

Unfortunately Foerste had discovered only about half of the problem; it becomes increasingly apparent from the numbers of central Appalachian Upper Ordovician specimens which I have collected that supposedly mature specimens from the same

horizon may be ovate or oblique (Pl. 25, fig. 1, and Pl. 26, fig. 6). Again, Hynd (1960) described quite significant morphological changes in the shape of *Pinctada albina* as a result of environmental influences. He did not relate these changes in the character of the shell to any clearly defined environmental conditions. Added to the characteristic allometric growth that invariably shows a pronounced oblique juvenile shell, middle-sized erect specimens and large obtuse forms, Hynd (1960) found that pterioid shells assumed two extreme shapes as the result of environmental influences. One group, found in a "rocky environment" and attached to a hard subsurface, exhibits a relatively stronger projection of the anterior margin and the posterior wing; the posteroventral margin does not project and the shell form is obtuse. The second group, presumably the sandy-bottom dwelling, inner sublittoral specimens, shows no noticeable projection of the anterior margin or of the posterior wing; rather, the posteroventral margin projects strongly and the shell form is oblique or erect. Pterioids from the central Appalachian Upper Ordovician rocks exhibit the obtuse and oblique shell forms as a function of size and possibly of ecological control.

Pterinea (*Caritodens*) *demissa* is one of the most widespread faunal elements in the central Appalachian Upper Ordovician strata, but is abundant only in southwestern Virginia, bivalve faunal province III (Fig. 17 and Table 3, loc. 141, 147, 149, 184). Here it occurs in a silty mud with numerous *Zygospira recurvirostra, Ambonychia cultrata,* various trespostomatous Bryozoa and some *Hebertella sinuata,* all part of the Spiriferid Population of the *Zygospira–Hebertella* Community. In these localities where *P.* (*C.*) *demissa* is common both right and left valves are found. In the more northerly exposures where fewer valves are found, only the more convex left valve occurs. Bassler (1919), Foerste (1910, 1914a, 1924) and Ruedemann (1926) have figured only left valves, and Ruedemann (1926, p. 26) thought that the right valve may have been in some way less resistant. The right valves may have been more delicate, more easily fragmented by currents, and thus more readily lost through the effects of diagenesis and compaction. Another possibility, perhaps less likely, is that of differential shell transport. The plate-shaped, probably lighter right valves may have been more easily winnowed and scattered by waves and currents, whereas the convex left valves, larger and somewhat heavier, would tend to remain aggregated and be preserved essentially in place.

Inferences as to life habitats of the central Appalachian Upper Ordovician *P.* (*C.*) *demissa* come from the spare literature available on Recent pterioids. Although there is a fair amount of data concerning their anatomy, there are few references to ecology and environmental setting. Modern pterioids appear to live in a variety of shallow and deep water environments, although they appear most prolific in the inner sublittoral. Attached to a firm sandy substratum or solid object (e.g., reefs, rocks, pilings) by the convex right valve, they exhibit a pronounced byssal notch in the right valve. Newell (1937, p. 18–20) discussed the enigma that no known Paleozoic pterioids or pectinoids have a markedly convex right valve. As is the case in the Ordovician *P.* (*C.*) *demissa*, the right valve is only slightly convex and is, in fact, partially concave at the margin. The byssal notch in the right valve of *P.* (*C.*) *demissa* is no more pronounced than that in the left valve. Whether these Ordovician pterioids rested on their convex left or "flat" right valve remains unknown.

The probable environmental setting for *P.* (*C.*) *demissa* is an inner sublittoral, quiet, non-turbid environment where wave and current energy was only strong enough

to winnow and scatter the more delicate right valves. The pterioids definitely thrived away from the more northerly influx of clastic terrigenous sediments. There is no significant geographic trend in the shape of *P.* (*C.*) *demissa* shells, although there are more numerous oblique shells in the southwestern Virginia localities where the pterioids are most abundant. This is the more common shell form for Recent pterioids living on "sandy" bottoms and not attached to a hard substratum. The pronounced alate form apparently common in the Upper Ordovician of southeastern Canada and figured by Foerste (1914a, 1924) is, however, not common in the central Appalachian clastic facies or in the New York Upper Ordovician Lorraine Group (Ruedemann, 1926, p. 25).

Subclass PALAEOHETERODONTA
Order ACTINODONTOIDA
Superfamily MODIOMORPHACEA
Family MODIOMORPHIDAE
Genus *MODIOLOPSIS*

Modiolopsis modiolaris (Conrad, 1838)

Plate 31, figures 1-3; plate 32, figures 1-3; Plate 33, figures 1-3; Plate 34, figures 1-3; plate 35, figures 1-4

Pterinea modiolaris Conrad, 1838, p. 118.

Cypricardites modiolaris (Conrad). Conrad, 1841, p. 52. Emmons, 1842, p. 403, [?]fig. 4; p. 405, fig. 114.2.

Cypricardites augustifrons Conrad, 1841, p. 52. Emmons, 1842, p. 405, fig. 114.1.

Cypricardites ovata Conrad, 1841, p. 52.

Modiolopsis modiolaris (Conrad). Hall, 1847, p. 294, pl. 81, fig. 1a-1g, [?]pl. 82, fig. 1. Billings, 1856, p. 44, fig. 8. Billings, 1863, p. 213, fig. 217. Ulrich, 1894, p. 481, figs. 37a, [?]37b. Bassler, 1909, pl. 14, fig. 8. Foerste, 1914a, p. 281, pl. 3, fig. 1; pl. 5, figs. 1, 2. [not]Hall and Whitfield, 1875, p. 83, pl. 2, fig. 17. Bassler, 1919, p. 286, pl. 58, fig. 12. Stewart, 1920, p. 34, pl. 3, fig. 1.

Lysonia submodiolaris (d'Orbigny). Emmons, 1855, p. 171, pl. 17, figs. 8, 8a.

Modiodesma modiolare (Conrad). Ulrich, 1924, p. 191, pl. 31, fig. 1; pl. 32, figs. 1-3; pl. 33, figs. 3-6. Ruedemann, 1925a, pl. 6. Ruedemann, 1926, p. 32, pl. 4.

Modiodesma modiolare var. *augustifrons* (Conrad). Ulrich, 1924, p. 189, pl. 32, figs. 4, 5. Ruedemann, 1926, p. 34, fig. 11.

Modiodesma modiolare var. *brevoir* Ulrich, 1924, p. 189. Ruedemann, 1926, p. 34.

[?]*Modiodesma scapha* Ulrich, 1924, p. 189, pl. 33, figs. 1, 2.

[?]*Orthodesma* sp.? Butts, 1941, p. 114, pl. 96, figs. 19, 20.

[?]*Rhytimya* sp.? Butts, 1941, p. 127, pl. 100, fig. 1; p. 128, pl. 100, figs. 14, 15.

[?]*Whiteavesia* sp.? Butts, 1941, p. 127, pl. 100, fig. 16.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of large size (median length of 154 specimens, 51 mm, median height of 171 specimens, 20 mm), inflated, equivalved, extreme posterior elongation. Shape variable, height varying between 19 and 62 per cent of the length (median of 120 specimens 42 per cent), much of shape variation results from tectonic distortion (Pl. 35, fig.

4; cf. Ulrich, 1894, p. 481, figs. 37a, b). Byssal sinus shallow, on ventral margin, toward anterior. Umbones rounded, near anterior margin; umbonal ridge faint, broadly rounded, flattens toward posterior. Anterior margin sharply rounded, narrow; posterior margin broadly rounded, expanded. Surface sculpture of fine concentric striae, preserved as external mold, over entire shell, most prominent at postero- and anterodorsal margins. Edentulous. Ligament broad, elongate, straight to moderately curved, opisthodetic, possibly partially internal. Anisomyarian, anterior adductor large, subcircular to elongate, narrowing at dorsal edge; posterior adductor two times larger than anterior, very faint, subcircular. Pedal retractors small, elongate, directly above anterior adductor. All other internal features unknown. Shell microstructure and mineralogy unknown.

Materials. The description is based on over 850 specimens from south-central Pennsylvania to northern Tennessee deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Modiolopsis modiolaris* is tentative pending a restudy of *Modiolopsis* Hall, *Orthodesma* Hall and Whitfield, and *Cymatonota* Ulrich.

Hall (1847, p. 297) combined *Pterinea modiolaris* (= *Cypricardites modiolaris*) Conrad, *Cypricardites augustifrons* Conrad and *Cypricardites ovata* Conrad to form *Modiolopsis modiolaris,* which was defined as the type of Hall's new genus *Modiolopsis.* In the definition of *M. modiolaris*, Hall placed a great deal of emphasis on the extreme shape variability of the New York Ordovician specimens. This variability was thought to result from "natural" and "compressional" forces. Hall probably attributed to "natural forces" the distinct shape variation between forms found in shales and those in sandstones, although he failed to mention specifically what the characteristic changes were. The secondary tectonic or "compressional" forces that altered the original shell shape were documented by Ulrich (1894, p. 481, figs. 37a, b; Pl. 35, fig. 4, this paper). Distorted *M. modiolaris* and other associated faunal elements are common at most localities in the central Appalachians.

Ulrich (1924, p. 183) reviewed Hall's type material and attempted to redefine *M. modiolaris* but incorrectly made it the type of a new genus *Modiodesma.* Ulrich claimed that *Modiolopsis modiolaris* had to be removed from the genus *Modiolopsis* because it did not conform to Hall's generic definition. *Modiodesma modiolaris* must be considered a junior objective synonym of *Modiolopsis modiolaris.* It is certainly possible that Hall's material contained more than one species, but I doubt that Ulrich's division of *Modiolopsis modiolaris* into four separate species representing three genera can be substantiated. I do feel, however, that Hall's (1847) pl. 82, fig. 1 is probably not *Modiolopsis modiolaris.* Whether it is another species of *Modiolopsis* (*M. milleri*?) or a species of *Colpomya* must await a more complete taxonomic revision.

Newell et al. 1969 have placed the genus *Modiodesma* in synonymy with *Modiolopsis* and have added a number of junior subjective synonyms; one is the genus *Orthodesma* Hall and Whitfield, which has been identified previously in the central Appalachian Upper Ordovician rocks as occurring with *M. modiolaris* (Foerste, 1914a, p. 284-285). Hall and Whitfield (1875, p. 93) defined *Orthodesma* as differing from *Modiolopsis* in the absence of hinge teeth; Ulrich (1894, p. 516) emphasized the edentulous nature of *Orthodesma* and its close relationship to *Modiolopsis,* but felt that the elongate outline, coarser concentric striae and slightly gaping valves were typi-

cal of *Orthodesma*. I have found in the central Appalachian material that misidentification of *Modiolopsis modiolaris* as *Orthodesma rectum* or *O. nasuta* is simply a function of distortion and selective preservation. The coarser concentric striae are preserved only as an external mold of *M. modiolaris*, and the distortion gives rise to the elongate outline and the gaping valves. I am in complete agreement, however, with John Pojeta of the U. S. Geological Survey (pers. comm.) that some gaping, elongate *Orthodesma*-like bivalves in the Ordovician are distinct from what I believe to be deformed *Modiolopsis*. A complete review of the Family Modiomorphidae Miller 1877 (=Modiolopsidae Fischer 1887) should resolve these problems.

Modiolopsis modiolaris is one of the most common central Appalachian Upper Ordovician faunal elements and is abundant from south-central Pennsylvania to south-central Virginia, bivalve faunal province II (Fig. 17). Associated faunal elements are normally *Ambonychia praecursa* and, rarely, *Orthorhynchula linneyi* (Ruedemann, 1925a, p. 6; Pl. 2, this paper), both in the Modiolopsid and Rhynchonellid Populations of the *Orthorhynchula–Ambonychia* Community. Patches of abundant *M. modiolaris* occurring alone appear common in central Virginia. The substratum is usually a muddy silt-sand, and the patches of concentrated, exclusively *M. modiolaris* are found in a muddier sediment. But most of the *M. modiolaris* are not clumped but are scattered over the bedding plane, where the valves are often articulated and in various degrees gaping.

In southwestern Virginia and northern Tennessee, bivalve faunal province III (Fig. 17), *M. modiolaris* is a less dominant faunal element, usually smaller (length normally less than 30 mm), less notably elongate and more rectangular (Pl. 35, fig. 2). It resembles *M. concentrica*; but I feel that these morphological differences are slight in light of the poor preservation of the southern material and the present wide range of shape variation permitted in *M. modiolaris*. The substratum is a silty mud in southwestern Virginia and the common associated faunal elements are *Ambonychia cultrata*, *Zygospira recurvirostra* and *Dekayia* in the Spiriferid Population of the *Zygospira–Hebertella* Community (Table 3, loc. 149, 151, 141). In the lime muds of northern Tennessee, *M. modiolaris* is found with abundant *Zygospira recurvirostra*, *Hebertella sinuata* and a few *Ambonychia radiata*?.

Scattered modiolopsids, possibly *M. sinuata* (= *M. anodontoides*?; Pl. 32, fig. 2) are found with abundant *Onniella multisecta*, crinoids and *Lyrodesma poststriatum* from the Orthid–Crinoid Population of the *Sowerbyella–Onniella* Community in north-central Pennsylvania, bivalve faunal province I (Fig. 17). A few small *Colpomya* and *Cymatonota* (= ?*Psiloconcha*) are occasionally found with abundant crinoids in the same general area. Very poorly preserved modiolopsids occur along the eastern edge of the Reedsville exposures in north-central Virginia bivalve faunal province I (loc. 167, 168, 169), where they are found with abundant *Rafinesquina* "*alternata*", numerous pleurotomariacean gastropods and a few *Cyrtodonta*? (Pl. 37, figs. 1-3), part of the Strophomenid Population of the *Sowerbyella–Onniella* Community. The state of preservation of these modiolopsid-like bivalves precludes even a tentative generic assignment.

The environmental setting and life habits of *M. modiolaris* probably were much like those of some recent species of *Modiolus*. One, *Modiolus rectus*, found along the west coast of the United States, is bysally attached in the muddy silts and sands of quiet water, nearshore environments. The mussel is usually solitary and occasionally is

found covering a fairly extensive mud-silt flat, or muddy substratum in 5 to 15 meters of water. It is embedded vertically in the mud with just the posterior tip of the shell projecting above the surface (Fitch, 1953, p. 48; Keen, 1958, p. 56). Small clumps or patches of the related *Modiolus modiolus* have also been reported by Kuderskii (1962) from the inner sublittoral waters of Onega Bay, the White Sea, U.S.S.R.

The central Appalachian Upper Ordovician *M. modiolaris* is believed to have inhabited a quiet water, inner sublittoral environment, living bysally attached, usually solitary and partially embedded in the muddy silt substratum. Where abundant *M. modiolaris* is found alone and not in common association with *Ambonychia praccursa* there is usually a change in the substratum, from a muddy silt to a silty mud. This mud may place a limitation on the distribution of the subround ambonychiid but not on that of the more elongate modiomorphid which may, in fact, have lived embedded even more deeply in the muds. I have found little evidence to support the clumping of *M. modiolaris* into a shell bank. Rare large concentrations of articulated valves may reflect clumping or may have been produced by local current activity. Mortality-growth rate curves may provide further clues to the possibilities of transportation prior to burial.

M. modiolaris shows some evidence of infestations by *Polydora*-like worms; occasionally a few specimens exhibit a characteristic, irregular "U"-shaped worm tube at the approximate position of the inhalent current (Pl. 31, fig. 1). This infestation is never extensive and probably had little influence on the distribution of *M. modiolaris*. And most often the posterior portion of the shell extends beyond the tube, probably indicating an adequate relining of shell material over the tube. One interesting note is that collections of *M. modiolaris* in the Peabody Museum from the Upper Ordovician of the Cincinnati region occasionally show identical inhalent worm tubes. Boekschoten (1966, p. 354), working along the Dutch tidal flat, described Recent *Polydora* tubes at the posterior margins of some *Cardium edule*, which appears to be indicative of attack in living position. Only where the valves were separated and lying loose on the substratum were they bored over the entire surface.

[?]Order TRIGONIOIDA
[?]Superfamily LYRODESMATACEA
[?]Family LYRODESMATIDAE
Genus *ISCHYRODONTA*

Ischyrodonta truncata Ulrich, 1890
Plate 27, figures 3-6; plate 28, figures 1-6; plate 29, figures 1-6; plate 30, figures 1-6

[?]*Modiolopsis truncatus* Hall, 1847, p. 296, pl. 81, figs. 3a, b. Hall and Whitfield, 1875, p. 86, pl. 2, fig. 13.

[?]*Lysonia subtruncata* (d'Orbigny). Emmons, 1855, p. 171, pl. 17, fig. 4.

Ischyrodonta truncata [not Hall, 1847] Ulrich, 1890, p. 174, figs. 11a-11e. Ulrich, 1893, p. 672, figs. 1a-1e.

[?]*Ischyrodonta ovalis* Ulrich, 1892, p. 242, fig. 27. Ulrich, 1893, p. 674, pl. 54, figs. 12-15. Ulrich, 1894, p. 477, fig. 35-I.

[?]*Ischyrodonta decipiens* Ulrich, 1893, p. 673, pl. 45, figs. 16-19.

[?]*Modiolodon truncatus* (Hall). Ulrich, 1893, p. 656, pl. 51, figs. 9, 10. Bassler, 1919,

p. 288, pl. 57, fig. 25. Ruedemann, 1926, p. 39. Butts, 1941, p. 127, pl. 100, figs. 2, 3.

[?]*Eurymya? truncata* (Hall). Ulrich, 1894, p. 512.

[?]*Modiolopsis* sp.? Butts, 1941, p. 127, pl. 100, figs. 12, 13.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size (median length of 78 specimens, 29 mm; median height of 107 specimens, 17 mm), inflated, inequivalved, broad, posterior expansion. Shape sub-trapezoidal, variable, height varying between 50 and 70 per cent of the length (median of 73 specimens, 61 per cent); distance umbo to anterior margin varying between 22 and 45 per cent of total shell length (median of 73 specimens, 32 per cent). Byssal sinus very faint. Anterior margin broadly rounded; posterior margin flattened, wide, intersection with hinge line sharply rounded. Umbones prominent, sharp, gently pointed toward anterior, curved in toward hinge line; umbonal ridge broad, subangular. Surface sculpture prominent, concentric striae, coarse, widely spaced. Cardinal teeth usually two, radiating from beneath umbo; lateral teeth unknown. Ligament duplivincular, two or three longitudinal striae, narrow, internal, amphidetic (Pl. 30, fig. 6). Anisomyarian; anterior adductor muscle large, elongated dorsoventrally, subround, with coarse longitudinal furrows; posterior adductor faint, subcircular, twice as large as anterior muscle. Pedal retractor muscle prominent, small, rounded, directly above but separated from anterior adductor. All other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on over 250 specimens from Pennsylvania to Tennessee deposited in the Peabody Museum.

Discussion. The assignment of these central Appalachian Upper Ordovician specimens to *Ischyrodonta truncata* is tentative pending a complete taxonomic restudy of *Ischyrodonta*, *Modiolodon*, *Ortonella*, *Cyrtodonta* and *Modiolopsis*. The strong, well-defined cardinal teeth and the duplivincular ligament presumably set *Ischyrodonta* apart from *Modiolopsis*. The lack of any posterior lateral teeth probably separates it from *Cyrtodonta* and *Ortonella*, but *Ischyrodonta* Ulrich (1890, p. 173) and *Modiolodon* Ulrich (1893, p. 652; 1894, p. 521) had been considered indistinguishable.. However John Pojeta (pers. comm.) has informed me that silicified topotypic *Modiolodon* material does not show a duplivincular ligament.

Bassler (1919, pl. 57, fig. 25) and Butts (1941, pl. 100, figs. 2, 3, 12, 13) have figured poorly preserved specimens from the central Appalachian Upper Ordovician rocks, which they called *Modiolodon truncatus* and *Modiolopsis* sp.?, that resemble the specimens I have collected from the same area. Ruedemann (1926, p. 39), however, claimed that *M. truncatus* is exclusively an Ohio Valley species and that the New York, Appalachian and Canadian specimens misidentified as this species are really *Ischyrodonta* (= *Anodontopsis*) *unionoides*, a possibility that had been touched upon briefly by Hall and Whitfield (1875, p. 86). The reasons for his reassignment are not clear, although Ulrich (1890, p. 173; 1894, p. 521) suggested the supposedly thicker shell and well-preserved pedal muscle scars, common to the Appalachian specimens, are more characteristic of *Ischyrodonta* than *Modiolodon* or *Cyrtodonta*.

Ischyrodonta unionoides has been reported frequently from the Upper Ordovician rocks of eastern North America (Ulrich, 1893; Foerste, 1914a, 1924; Bassler, 1919;

Stewart, 1920; Ruedemann, 1926), but all the figured specimens are considerably more ovate than the specimens I have collected and have assigned to *I. truncata*. In fact, *I. truncata* seems to present something of an intermediate subtrapezoidal shape between the rounded *I. unionoides* and the notably elongate *I. elongata* Ulrich (1890), *I. miseneri* Ulrich (1893) and *I. modioliformis* Ulrich (1893).

Ischyrodonta truncata is one of the most common and widespread faunal elements in the central Appalachian Upper Ordovician. It is most abundant from south-central Pennsylvania to southern Virginia, bivalve faunal province II (Fig. 17), and is associated with two distinct faunal populations. In one case *O. linneyi* from the Rhynchonellid Population of the *Orthorhynchula–Ambonychia* Community is the most abundant associated faunal element. *I. truncata* is also found associated with *Tancrediopsis cuneata, Lingula*? and *Plectonotus*? sp., part of the Linguloid Population of the *Orthorhynchula–Ambonychia* Community, although *O. linneyi* rarely occurs with these. The substratum in both cases is a muddy silt-fine sand. Smaller numbers of *I. truncata* are found with abundant *Rafinesquina* "*alternata*", *Onniella multisecta*, crinoids, *Hallopora*, and *Lyrodesma poststriatum*, part of the Orthid-Crinoid Population of the *Sowerbyella–Onniella* Community, in north-central Pennsylvania (Table 3, loc. 77-A, 110) in a fine muddy silt, and in southwestern Virginia and northern Tennessee (loc. 141, 147, 133, 135, 139) with abundant *Zygospira recurvirostra*, *Pterinea* (*Caritodens*) *demissa*, *Murchisonia*? and various trespostomatous Bryozoa, part of the Spiriferid Population of the *Zygospira–Hebertella Community*, in a fine silty mud.

The life habits of *I. truncata* may have resembled those of some Recent *Modiolus* (especially *M. capax*), to which *I. truncata* shows a superficial resemblance. The environmental setting probably was similar to that proposed for *Modiolopsis modiolaris*, in which the mussel lived byssally attached to a silt-sand substratum, partially submerged in a quiet, semi-protected, inner sublittoral environment. The distribution rarely shows clumping of individuals. Sardeson (1924) provided evidence for the possibility of an infaunal habit for some mid-continent *Cyrtodonta*, to which *I. truncata* shows at least some resemblance in shape, musculature and cardinal dentition. *I. truncata* may therefore have assumed a partially submerged habit especially in the nearer shore, possibly more turbulent environments. Some tolerance for temporary changes in salinity may be indicated by its association with abundant *Lingula*? and *Tancrediopsis cuneata*. Association with abundant *O. linneyi* probably points to a more normal marine environment. Locally common in *I. truncata*, when associated with *O. linneyi*, is the preservation of what appears to be worm tubes at the inhalent opening (Pl. 28, fig. 3; Pl. 29, fig. 3). Tubes of this type are also commonly found preserved on *O. linneyi* valve margins at the probable sites of inhalent currents (Pl. 14, fig. 1). The ecological significance of this infestation was probably minimal.

Genus *LYRODESMA*

Lyrodesma poststriatum (Emmons, 1842)
Plate 44, figures 1-7

Nuculites poststriatus Emmons, 1842, p. 399, fig. 4.

Nucula poststriata (Emmons). Hall, 1847, p. 151, pl. 34, figs. 2a, b, [?]p. 301, pl. 82, figs. 10a, b.

Cardiomorpha poststriata (Emmons). Emmons, 1855, p. 175, pl. 17, fig. 22.
Lyrodesma poststriatum (Emmons). Billings, 1863, p. 176, figs. 167a, b. Nicholson, 1875, p. 36, fig. 11b. Foerste, 1914a, p. 306. Stewart, 1920, p. 26, pl. 4, fig. 5. Foerste, 1924, p. 169, pl. 25, fig. 10a, b; pl. 43, fig. 9.
[?]*Lyrodesma cannonense* Ulrich, 1894, p. 601, pl. 42, figs. 6-8.
[?]*Lyrodesma schucherti* Ruedemann, 1912, p. 103, pl. 6, fig. 5.
[?]*Lyrodesma poststriatum elongatum* Stewart, 1920, p. 26, pl. 4, fig. 5. Foerste, 1924, p. 170, pl. 22, fig. 8.
Lyrodesma poststriatum manitoulinense Foerste, 1924, p. 170, pl. 43, fig. 5.

Description Based on Specimens from the Central Appalachian Upper Ordovician. Shell of medium size, pronounced posterior elongation (median length of 19 specimens, 17 mm; median height, 11 mm). Shape variable, height ranging from 61 to 70 per cent of length (median of 19 measured specimens, 62 per cent). Surface sculpture of fine concentric striae, faint except near edges of valves, about six prominent coarse radial ribs at posterodorsal edge of shell. Prominent schizodont teeth, normally eight; well-marked longitudinal striae on each tooth (Pl. 44, fig. 4); teeth not uniform in size, notable anterior and slight posterior decrease in size away from the umbo. Resilifer absent, ligament area otherwise unknown. Anterior and posterior adductor muscle scars rounded, posterior slightly more elongate. Pedal muscle scars rounded, posterior pedal scar slightly larger and more elongate than anterior. Pallial line with distinct impression of a small pallial sinus, posteroventral, preserved as internal mold on two specimens (Pl. 44, fig. 5); other internal features unknown. Original shell microstructure and mineralogy unknown.

Materials. The description is based on about 30 specimens from central Pennsylvania deposited in the Peabody Museum.

Discussion. Sixteen species and subspecies described from the Middle and Upper Ordovician strata of North America have been assigned to the genus *Lyrodesma* (see Wilson, 1956, p. 64, for a concise generic description). This grouping of species can be informally subdivided into three morphological groups on the basis of shell size, shape variation (height to length ratios) and the degree of posterior expansion. Table 21 outlines these three groups. Stewart (1920, p. 26) also mentioned that there ap-

table 21. An informal morphological grouping of previously defined *Lyrodesma* species. The three groups are qualitative and designed only for a clearer understanding of the shape variability within the central Appalachian Upper Ordovician specimens.

1. Small size, oval, no distinct posterior expansion	2. Medium size, suboval, pronounced posterior expansion	3. Large size, subellipsoidal extreme posterior expansion
Lyrodesma cincinnatiense	*Lyrodesma poststriatum*	*Lyrodesma major*
L. acuminatum	*L. poststriatum elongatum*	*L. postplanum*
L. acuminatum intermedium	*L. poststriatum manitoulinense*	*L. huguesensis*
L. planum	*L. cannonense*	
L. inoratum	*L. schucherti*	
L. conradi		
L. grande		
L. subplanum		

peared to be three distinct subgroups of the genus *Lyrodesma*, based on noticeable differences in height-length ratios; but she did not discuss the distinguishing characteristics of these groups. Instead, she mentioned only a characteristic "type" for each group.

Most of the Appalachian *Lyrodesma* specimens can be assigned to *Lyrodesma poststriatum* of subgroup 2 (Table 21), but a few specimens show morphological characteristics that appear to typify one of the other subgroupings and thus may belong to one or more other species. These latter specimens, because they are rare, have not been described. In fact, the shape variation within the genus itself remains poorly known and a complete resurvey of *Lyrodesma* morphological variability should be undertaken. Thus the three subgroups are not intended as taxonomic groupings in this report, but rather are introduced as a means of emphasizing overall size and shape variability especially with regard to the most common central Appalachian form.

Lyrodesma poststriatum is common in central Pennsylvania, (loc. 122, 37, 35, 52, and 97), where it occurs with *Praenucula levata*, *Ctenodonta*? *pulchella*, crinoids and lesser numbers of *Rafinesquina* "*alternata*" and *Onniella multisecta*. The substratum is a finely laminated silt or mud, and the most likely environmental setting appears to be in quiet, offshore waters. *Lyrodesma* is unique in that it is an Early Paleozoic siphonate bivalve. By analogy with Recent siphonate forms, where depth of burrowing appears directly related to the depth of sinuosity of the pallial sinus, *Lyrodesma* appears to have been a shallow infaunal form. I have also collected a few *Lyrodesma* specimens from localities 189, 192, 195, and 203, where the fauna is dominated by *O. linneyi*, *Ambonychia praecursa* and *Modiolopsis modiolaris* in a muddy silt-sand. These rare specimens of *Lyrodesma* exhibit a more pronounced posterior expansion than the more abundant ones farther north, but unfortunately no pallial lines have been found preserved on these more posteriorly expanded specimens. I suspect, however, that specimens with a more deeply inset pallial sinus might be found, emphasizing a deeper infaunal habit in a more turbulent environment.

LOCALITY REGISTER

(includes only fossiliferous exposures, location given to nearest 0.5 mile.)

Locality	Peabody Museum Number	Description
1	(A-6324)	Road cut 1.0 mile s. of New Tripoli, Pa. along New Tripoli - Lynnville road.
2	(A-6325)	Road cut 1.5 miles n. of Lynnville, Pa. along New Tripoli - Lynnville road.
4	(A-6326)	Road cut 0.5 mile n. of Lynnville, Pa. along New Tripoli - Lynnville road.
9	(A-6327)	Road cut 1.5 miles s. of Pleasant Corners, Pa. along Pleasant Corners - Werley's Corner road.
11	(A-6328)	Road cut less than 0.5 mile s. of loc. 9.
12	(A-6329)	Road cut 0.5 mile s. of loc. 11.
15	(A-6330)	Road cut 1.5 miles w. of loc. 2 and 4 along a paved road leading sw. from New Tripoli, Pa.
16	(A-6331)	Road cut 1.0 mile n. of loc. 15.
17	(A-6332)	Road cut 1.0 mile s. of Lynnport, Pa. along Pa. Rt. 863.
18	(A-6333)	Road cut less than 0.5 mile s. of loc. 17.
19	(A-6334)	Road cut less than 0.5 mile s. of loc. 18.
22	(A-6335)	Road cut less than 0.5 s. of loc. 19.
23	(A-6336)	Road cut a few hundred yards n. of loc. 22.
24	(A-6337)	Road cut a few hundred yards n. of loc. 23.
25	(A-6338)	Road cut 2.0 miles s. of Jacksonville, Pa. along Pa. Rt. 737[?].
26	(A-6339)	Road cut 0.5 mile s. of loc. 25.
27	———	Road cut 1.5 miles w. of Albany, Pa. along Albany - Eckville road.
28	———	Road cut 2.5 miles w. of loc. 27.
30	(A-6340)	Quarry n. of Cedar Springs, Pa., junction Pa. Rts. 64 and 880.
31	(A-6341)	Road cut 1.0 mile se. of Rote, Pa. along Pa. Rt. 880.
32	(A-6342)	Road cut 0.5 mile n. of Loganton, Pa. along Pa. Rt. 880.
33	(A-6343)	Road cut 1.0 mile n. of Carroll, Pa. along Pa. Rt. 880.
34	(A-6344)	Road cut 1.0 mile s. of Rauchtown, Pa. along Pa. Rt. 880.

Locality	Peabody Museum Number	Description
34-A	(A-6345)	Quarry 1.0 mile s. of Rauchtown, Pa. within Pa. State Park grounds a few hundred yards e. of Pa. Rt. 880.
35	(A-6346 to A-6357)	Road cut 2.5 miles s. of Antes Fort, Pa. along Pa. Rt. 44.
36	(A-6358)	Road cut 2.0 miles se. of Collomsville, Pa. along Pa. Rt. 44.
37	(A-6359 to A-6363)	Road cut 0.5 mile n. of Bastress, Pa. along Pa. Rt. 654.
38	(A-6364)	Road cut 1.0 mile s. of Duboistown, Pa. along paved road through north limb of Raccoon Mountain.
39	(A-6365)	Quarry about 2.0 miles s. of Lamar, Pa. immediately n. of Pa. Rt. 780.
39-A	(A-6366)	Road cut a few hundred yards sw. of loc. 39.
42	(A-6369)	Road cut 3.5 miles n. of Livonia, Pa. along Livonia - Greenburr road.
43	(A-6370)	Road cut less than 0.5 mile n. of Livonia, Pa. along Livonia - Greenburr road.
44	(A-6371)	Road cut 0.5 mile n. of Rebersburg, Pa. along Rebersburg - Tylersville road.
45	(A-6372)	Road cut about 5.0 miles e. of Woodward, Pa. along Pa. Rt. 45.
47	(A-6374)	Quarry 1.0 mile s. of Nittany, Pa. along Pa. Rt. 445.
48	(A-6375)	Road cut 1.0 mile s. of junction of Pa. Rt. 192 and north-south paved road, north limb of Brush Mountain.
49	(A-6376)	Road cut 2.0 miles s. of loc. 48, south limb of Brush Mountain.
50	(A-6377)	Road cut 1.0 mile s. of Pleasant Gap, Pa. along Pa. Rt. 53.
51-A	(A-6379)	Road cut less than 0.5 mile n. of Bellefonte, Pa. along Pa. Rt. 53.
52	(A-6380)	Road cut 1.5 miles n. of Jacksonville, Pa. along Pa. Rt. 445.
60	(A-6381)	Quarry at junction of Pa. Rt. 53 and U. S. Rt. 322 at Potters Mill, Pa.
62	(A-6382)	Road cut about 1.0 mile se. of Reedsville, Pa. along U. S. 322.
63	(A-6383)	Road cut about 1.0 mile se. of Reedsville, Pa. along U. S. Rt. 322 Bypass.
64	(A-6384)	Road cut 2.5 miles n. of Belleville, Pa. along Pa. Rt. 305.
68	(A-6388)	Stream cut 1.0 mile nw. of Allensville, Pa.
69	(A-6389)	Road cut 3.5 miles ne. of Mill Creek, Pa. along Pa. Rt. 655.
70	(A-6390)	Road cut 1.0 mile s. of Franklinville, Pa. in Colraine State Park, s. of Pa. Rt. 45.
71	(A-6391)	Two small quarries 1.5 miles ne. of Lemont, Pa. along Lemont - Oak Hill road.
72	(A-6392)	Road cut at Baffalo Run, Pa. along U. S. 322.
73	(A-6393)	Road cut 0.5 mile n. of Centennial, Pa. along Centennial - Port Matilda road.

Locality	Peabody Museum Number	Description
75	(A-6395)	Railroad cut 1.0 mile se. of Tyrone, Pa. a few hundred yards s. of Pa. Rt. 350.
77	(A-6396)	Road cut 3.0 miles n. of Elberta, Pa. along Elberta - Culp road.
77-A	(A-6397)	Road cut a few hundred yards s. of loc. 77.
78	(A-6398)	Railroad cut 0.5 mile s. of Ganister, Pa. a few hundred yards e. of Pa. Rt. 866.
79	(A-6399)	Quarry 0.5 mile nw. of Royer, Pa. a few hundred yards off Pa. Rt. 866.
80	———	Quarry 1.5 miles nw. of Roaring Spring, Pa. along Pa. Rt. 164.
81	(A-6499)	Road cut 2.5 miles w. of Ore Hill, Pa. along Ore Hill - Sproul road.
82	(A-6400)	Road cut at Brumbaugh, Pa. at junction of Pa. Rts. 867 and 869.
83	(A-6401)	Road cut 2.5 miles ne. of Williamsburg, Pa. along Williamsburg - Huntingdon road.
84	(A-6402)	Road cut 2.5 miles se. of Clover Creek, Pa. along Pa. Rt. 164.
86	(A-6403)	Road cut 0.5 mile e. of Loysburg, Pa. along Pa. Rt. 868.
87	(A-6404)	Road cut 4.5 miles s. of Loysburg, Pa. along Pa. Rt. 36.
89	(A-6406)	Road cut a few hundred yards e. of Blue Mountain tunnel entrance, Pa. Turnpike.
91	(A-6407)	Road cut 8.5 miles e. of Tuscarora tunnel entrance, Pa. Turnpike.
92	(A-6408)	Road cut about 2.0 miles e. of Bedford, Pa., Pa. Turnpike.
93	(A-6409)	Road cut at junction of two unmarked, paved roads a few hundred yards e. of Sulfur Springs, Pa., western limb of Wills Mountain.
94	(A-6410)	Road cut 1.5 miles e. of Buffalo Mills, Pa., Buffalo Mountain.
95	(A-6411)	Road cut 2.0 miles n. of Fossilville, Pa. along unpaved road through southern edge of Buffalo Mountain.
96	(A-6412)	Road cut 2.0 miles e. of Bedford, Pa. along U. S. Rt. 30; a few hundred yards w. of junction of U. S. 30 and Pa. Rt. 326.
97	(A-6413)	Road cut 1.5 miles s. of Rainesburg, Pa. along unpaved Pa. Rt. 326.
98	(A-6414)	Road cut 6.5 miles s. of Loysburg, Pa. along Pa. Rt. 36.
99	(A-6415)	Road cut 1.0 mile w. of Everett, Pa., a few hundred yards off U. S. 30 on paved service road.
100	(A-6416)	Road cut 1.5 miles w. of Everett, Pa. along Everett - Ashcom road.
101	(A-6417)	Road cut 2.5 miles se. of McConnellsburg, Pa. along Pa. Rt. 16.
102	(A-6418)	Quarry 0.5 mile ne. of Knobsville, Pa. near junction of narrow, paved unmarked road and U. S. 522.

Locality	Peabody Museum Number	Description
103	(A-6419)	Road cut 3.0 miles e. of McConnellsburg, Pa. along U. S. 30.
104	(A-6420)	Road cut 2.0 miles w. of Fort Louden, Pa. along U. S. 30.
105	(A-6500)	Road cut 1.5 miles e. of Fannetsburg, Pa. along Fannetsburg - Upper Strasburg road.
106	(A-6421)	Road cut 1.5 miles w. of Upper Strasburg, Pa. along Pa. Rt. 533[?].
107	(A-6422)	Road cut 1.5 miles w. of Roxbury, Pa. along Pa. Rt. 641.
108	(A-6423)	Road cut 7.0 miles w. of Roxbury, Pa. along Pa. Rt. 641.
109	(A-6424)	Quarry 2.0 miles s. of Spring Run, Pa. along Pa. Rt. 641 immediately n. of Pa. Turnpike overpass.
110	(A-6425)	Road cut 4.5 miles e. of Neelytown, Pa. along Pa. Rt. 641.
111	(A-6426)	Road cut 2.0 miles e. of Orbisonia, Pa. along paved, unmarked road immediately n. of junction with U. S. 522.
112	(A-6427)	Road cut 2.0 miles w. of Mt. Union, Pa. along U. S. 22.
120	(A-6428)	Road cut 8.0 miles n. of Lemoyne, Pa. along U. S. 11 and 15.
121	(A-6429)	Road cut 1.5 miles n. of Doubling Gap, Pa. along Pa. Rt. 233.
122	(A-6430)	Road cut 3.0 miles e. of East Waterford, Pa. along partially paved East Waterford - New German Town road.
123	(A-6431)	Road cut 4.5 miles n. of Doylesburg, Pa. along Pa. Rt. 274.
124	(A-6432)	Road cut 4.5 miles n. of Clear Spring, Md., near Hanging Rock, Bear Pond Mountains.
125	(A-6433)	Road cut 1.5 miles e. of Thorn Hill, Tenn. along U. S. 255.
126	(A-6434)	Road cut 3.0 miles w. of Joppa, Tenn. along Joppa - Powder Springs road, Clinch Mountain.
127	(A-6435)	Road cut 1.5 miles s. of Rose Hill, Tenn. along Tenn. Rt. 33.
128	(A-6436)	Road cut 2.0 miles w. of Ridenour, Tenn. along Tenn. Rt. 61, Lone Mt.
129	(A-6437)	Road cut and stream cut 3.0 miles nw. of Yoakum Crossroad, Tenn. along unpaved road across Powell Valley and eastern edge of Cumberland Mountain; road parallels Davis Creek.
130	(A-6438)	Road cut and railroad cut 2.0 miles n. of Arthur, Tenn. along unpaved Arthur - Cumberland Gap road.
131	(A-6439)	Road cut immediately s. of Cumberland Gap, Tenn. along motel service road parallel to Tenn. Rt. 32 and U. S. 25E.
132	(A-6440)	Road cut 2.5 miles w. of Sycamore Hall, Tenn. along unpaved road from Sycamore Hall through Wallen Ridge that junctions with unmarked paved road 2.0 miles n. of Tazwell, Tenn.
133	(A-6441)	Road cut 2.0 miles sw. of Klondike, Tenn. along Tenn. Rt. 66.
134	(A-6442)	Road cut 2.0 miles nw. of Choptack, Tenn. along Tenn. Rt. 66.
135	(A-6443)	Road cut 7.0 miles se. of Kyles Ford, Tenn. along Tenn. Rt. 70, Clinch Mountain.

Locality	Peabody Museum Number	Description
136	(A-6501)	Road cut 0.5 mile s. of Unthanks, Va. along Va. Secondary Rt. 758.
137	(A-6444)	Road cut 1.0 mile w. of U. S. 58 near Hagan, Va. along the Hagan - Smiley road.
138	(A-6445)	Road cut 3.5 miles se. of Bowling, Va. along Va. Primary Rt. 70 and U. S. Alt. 58.
139	(A-6446)	Road cut 2.5 miles nw. of Blackwater, Va. along Va. Primary Rt. 70 and 798[?], Powell Mountain.
140	(A-6447)	Road cut 3.0 miles n. of Mendota, Va. along unpaved Mendota - Collinwood, Va. road.
141	(A-6448)	Road cut 3.5 miles nw. of Pattonsville, Va. along U. S. 421 and 58, Powell Mountain.
142	(A-6449)	Road cut 1.5 miles nw. of Stickleyville, Va. along U. S. 421 and 58, Wallen Ridge.
143	(A-6450)	Stream cut 1.0 mile nw. of Pennington Gap, Va. a few hundred yards ne. of U. S. 421.
144	(A-6451)	Road cut 1.5 miles se. of Olinger, Va. along paved, unmarked road that junctions with U. S. Alt. 58.
145	(A-6452)	Road cut 1.0 mile s. of Rockdell, Va. along Va. Primary Rt. 80, Clinch Mountain.
147	(A-6453)	Road cut 1.5 miles se. of Mt. Gate, Va. along Va. Primary Rt. 16, Clinch Mountain.
148	(A-6454)	Road cut 12.5 miles n. of Marion, Va. along Va. Primary Rt. 16, Walker Mountain.
149	(A-6455)	Road cut about 10 miles n. of Broadford, Va. along unpaved Va. Primary Rt. 91, Clinch Mountain.
150	(A-6456)	Road cut 6.0 miles nw. of Chilhowie, Va. along Va. Primary Rt. 107, Walker Mountain.
151	(A-6457)	Road cut a few hundred yards s. of Walker Mountain lookout tower along Va. Secondary Rt. 621, near junction with U. S. 21 and 52.
152	(A-6458)	Road cut 1.5 miles s. of Rocky Gap, Va. along U. S. 21 and 52, Wolf Creek Mountain.
153	(A-6459)	Road cut 2.0 miles se. of Bluefield, W. Va. along U. S. 21 and 52, East River Mountain.
160	(A-6460)	Road cut about 10 miles s. of Wardensville, W. Va. along unpaved road parallel to Waites Run, Great North Mountain.
161	(A-6461)	Road cut 3.0 miles e. of Lost City, W. Va. along W. Va. Rt. 59, Great North Mountain.
162	(A-6462)	Road cut 4.0 miles n. of Liberty Furnace, Va. along unpaved Liberty Furnace - Perry road.
163	(A-6463)	Road cut 1.0 mile w. of Cootes Store along Va. Primary Rt. 259 (Brock's Gap).
164	(A-6464)	Road cut about 15 miles w. of Harrisonburg, Va. at Harrison's Gap, along Harrisonburg - Fulks Run road.

Locality	Peabody Museum Number	Description
165	(A-6465)	Road cut 0.5 mile w. of Basore, W. Va. along Basore - Mathias road.
166	(A-6466)	Road cut about 13 miles e. of Wardensville, W. Va. along Va. Primary Route 55, eastern limb of Great North Mountain.
167	(A-6467)	Road cut 3.0 miles s. of Water Lick, Va. along Va. Secondary Rt. 678, Massanutten Mountain.
168	(A-6468)	Road cut about 8 miles e. of New Market, Va. along U. S. 211 (New Market Gap).
169	(A-6469)	Road cut about 9 miles nw. of Shenandoah, Va. along unpaved road, eastern part of Massanutten Mountain.
170	(A-6470)	Road cut and railroad cut at Buffalo Gap, Va. along Va. Primary Rt. 254, Little North Mountain.
171	(A-6471)	Road cut 1.5 miles w. of McKinley, Va. along unpaved McKinley - Craigsville road.
172	(A-6472)	Road cut 7.0 miles nw. of Kerrs Creek, Va. along U. S. 60.
173	(A-6473)	Road cut 5.0 miles e. of junction of U. S. 60 and Va. Secondary Rt. 770, along Va. Secondary Rt. 770, North Mountain.
174	(A-6474)	Road cut 0.5 mile nw. of Eagle Rock, Va. along U. S. 220 e. of the James River.
175	(A-6475)	Road cut 0.5 mile sw. of Eagle Rock, Va. along U. S. 220 w. of the James River.
177	(A-6476)	Road cut 2.0 miles e. of Catawba, Va. along Va. Primary Rt. 311, Catawba Mountain.
178	(A-6477)	Road cut 2.5 miles sw. of Fagg, Va. along Va. Secondary Rt. 603.
179	(A-6478)	Road cut 3.0 miles s. of Radford, Va. along Va. Secondary Rt. 787, Ingle Mountain.
180	(A-6479)	Road cut 2.0 miles s. of Poplar Hill, Va. along Va. Primary Rt. 100, Walker Mountain.
181	(A-6480)	Road cut 5.5 miles s. of Mechanicsburg, Va. along Va. Secondary Rt. 738, Walker Mountain.
182	(A-6481)	Road cut 3.0 miles s. of Burkes Garden, Va. along Va. Secondary Rt. 623, southeastern limb of Garden Mountain.
183	(A-6482)	Road cut at Gose Mill, Va. along Va. Secondary Rt. 623, northwestern limb of Garden Mountain.
184	(A-6483)	Road cut 1.0 mile s. of Gratton, Va. along Va. Secondary Rt. 623, Rich Mountain.
185	(A-6484)	Railroad cut 1.0 mile n. of McCoy, Va. along Va. Secondary Rt. 652, Walker - Gap Mountain.
186	(A-6323)	Road cut 2.5 miles n. of Narrows, Va. along U. S. 460, East River Mountain.
187	(A-6485)	Road cut 1.5 miles n. of Mountain Lake, Va. along Va. Secondary Rt. 700, between Salt Pond and Doe Mountains.
188	(A-6486)	Road cut 3.5 miles s. of New Castle, Va. along Va. Primary Rt. 42.

Locality	Peabody Museum Number	Description
189	(A-6487)	Road cut 4.0 miles s. of Paint Bank, Va. along Va. Primary Rt. 311, southern limb of Little Mountain.
190	(A-6322)	Road cut 2.0 miles s. of Sweet Springs, W. Va. along Va. Primary Rt. 311, Peters Mountain.
191	(A-6488)	Road cut 0.5 mile se. of Cliffdale, Va. along Va. Secondary Rt. 616.
192	(A-6489)	Road cut 11.0 miles nw. of Eagle Rock, Va. along Va. Secondary Rt. 621 (or 613[?]), Rich Patch Mountain.
193	(A-6490)	Road cut 4.5 miles se. of Falling Spring, Va. along U. S. 220, Little Mountain.
194	(A-6491)	Road cut at Hot Springs, Va. paved road sw. of railroad station to Bacova Junction.
195	(A-6492)	Road cut 1.5 miles e. of junction of U. S. 220 and Va. Primary Rt. 39 along Va. Primary Rt. 39 e. of Warm Springs, Va.
196	(A-6493)	Road cut 2.0 miles n. of junction of U. S. 220 and Va. Primary Rt. 39 along U. S. 220 n. of Warm Springs, Va.
197	(A-6494)	Road cut 0.5 mile w. of Warm Springs, Va. along Va. Primary Rt. 39.
199	(A-6495)	Road cut 2.0 miles w. of Vanderpool, Va. along Va. Primary Rt. 84, Back Creek Mountain.
200	(A-6496)	Road cut 0.5 mile w. of Trimble, Va. along Trimble - Mustoe road, Jack Mountain.
201	(A-6497)	Road cut 2.5 miles e. of Hightown, Va. along U. S. 250.
202	(A-6498)	Road cut 1.0 mile w. of Hightown, Va. along U. S. 250.
203	(A-6301 to A-6321)	Road cut about 12 miles w. of Franklin, W. Va. along U. S. 33, eastern limb of North Fork Mountain.
204	———	Road cut 1.5 miles w. of loc. 203, west limb of North Fork Mountain.
205	———	Gas line cut 1.5 miles e. of Mouth of Seneca, W. Va.
206	———	Road cut 2.0 miles w. of Saumsville, Va. along Va. Secondary Rt. 600.
207	———	Quarry 2.0 miles n. of Lickdale, Pa. along Pa. Rt. 72 (Swatara Gap).

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PLATES

Abbreviations used in explanations:

YPM — Peabody Museum of Natural History,
Yale University, New Haven, Connecticut

Loc. — Locality

All illustrated specimens are deposited in the Peabody Museum of Natural History and were collected for this study. All magnifications are given in linear dimensions.

PLATE 1

(×5)

A-6304 — Disrupted laminae presumably due to biogenic reworking, phosphate grains seen as subround dark clasts—Locality 203. Section cut about 70 feet below Oswego–Reedsville contact.

PLATE 2

(×0.67)

A-6304 — Bedding plane with abundant *Ambonychia praecursa* and a few *Modiolopsis modiolaris* essentially "in place" and forming a small, clustered mussel-like bank. Viewed from underside of bedding plane. YPM 26065 — Locality 203.

PLATE 3

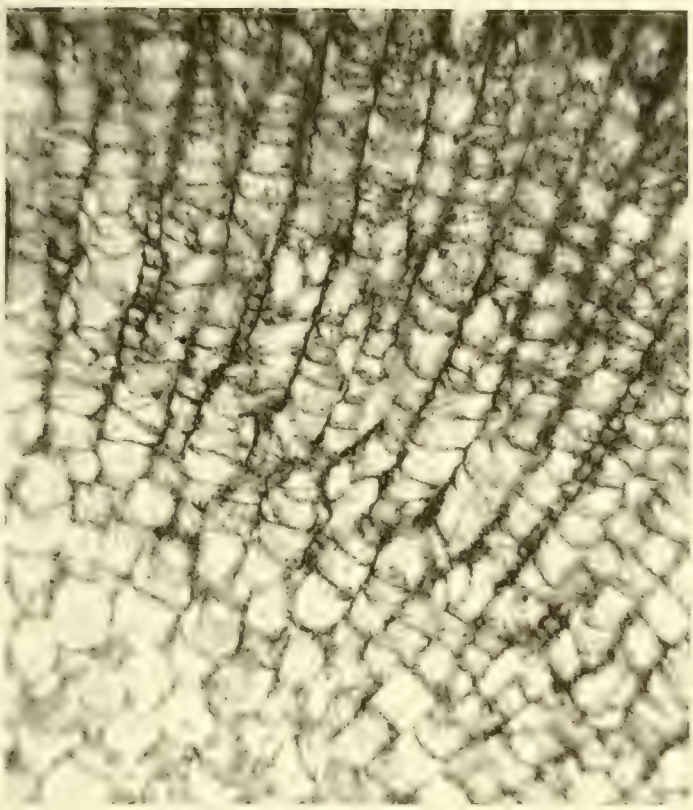
All figures are ×30 except fig. 3 (×50).

Figs. 1-3. Genus *Monticulipora* ..... p. 70

1. YPM 25848, Loc. 141 (A-6448), transverse section.
2. YPM 25849, Loc. 141 (A-6448), longitudinal section.
3. YPM 25848, Loc. 141 (A-6448), longitudinal section, same specimen as fig. 1.

Fig. 4. Genus *Dekayia* ..... p. 71

4. YPM 25850, Loc. 128 (A-6436), longitudinal section.



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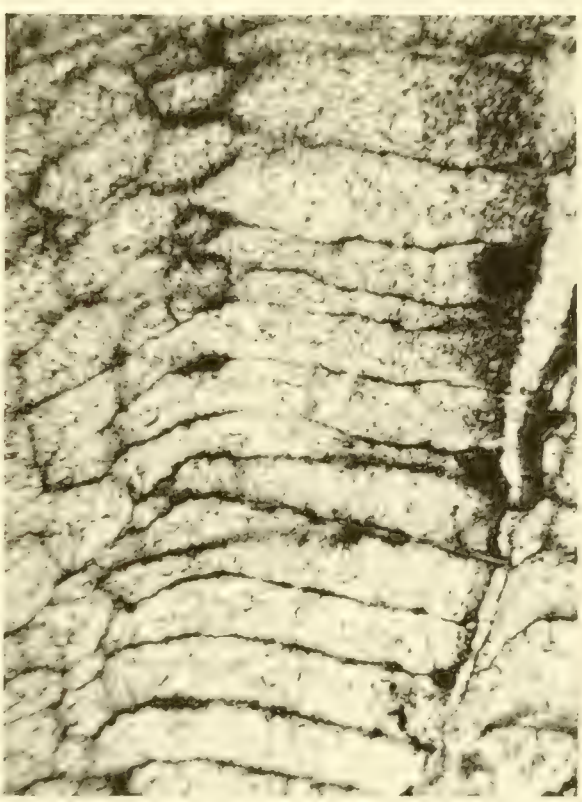

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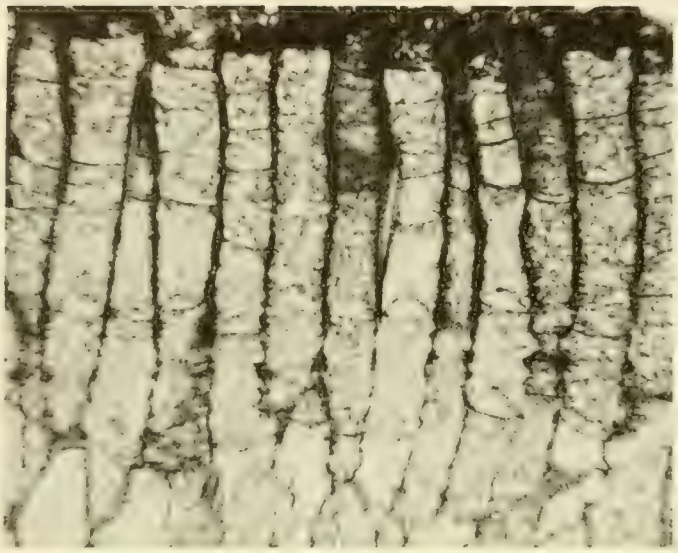

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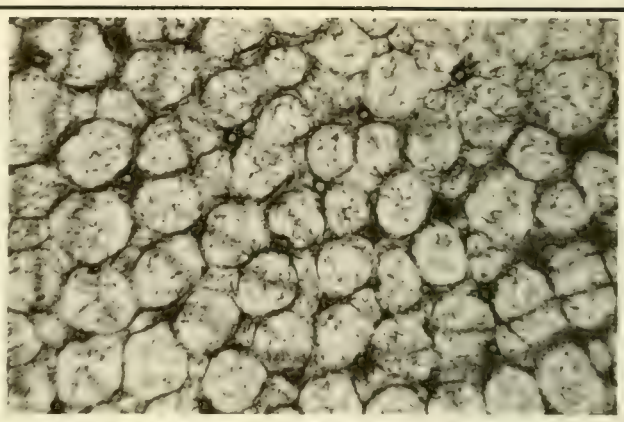

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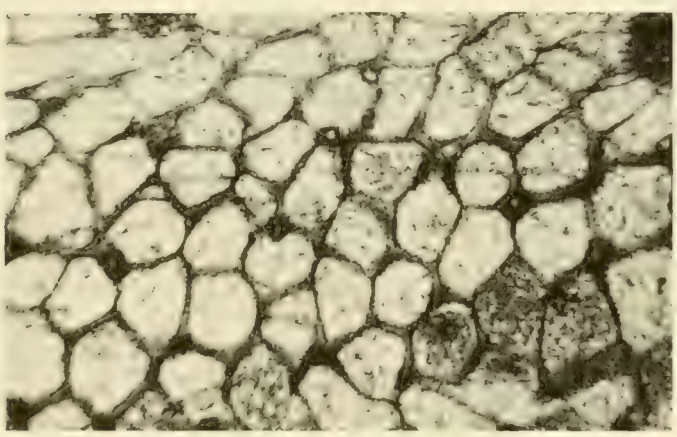

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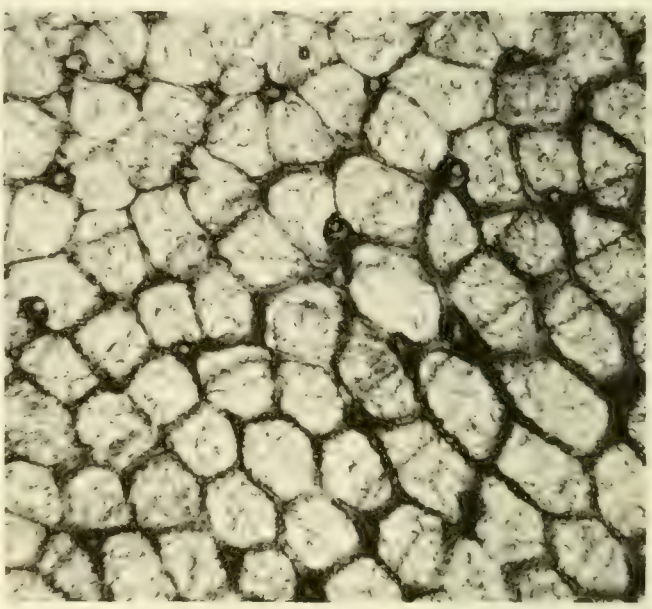

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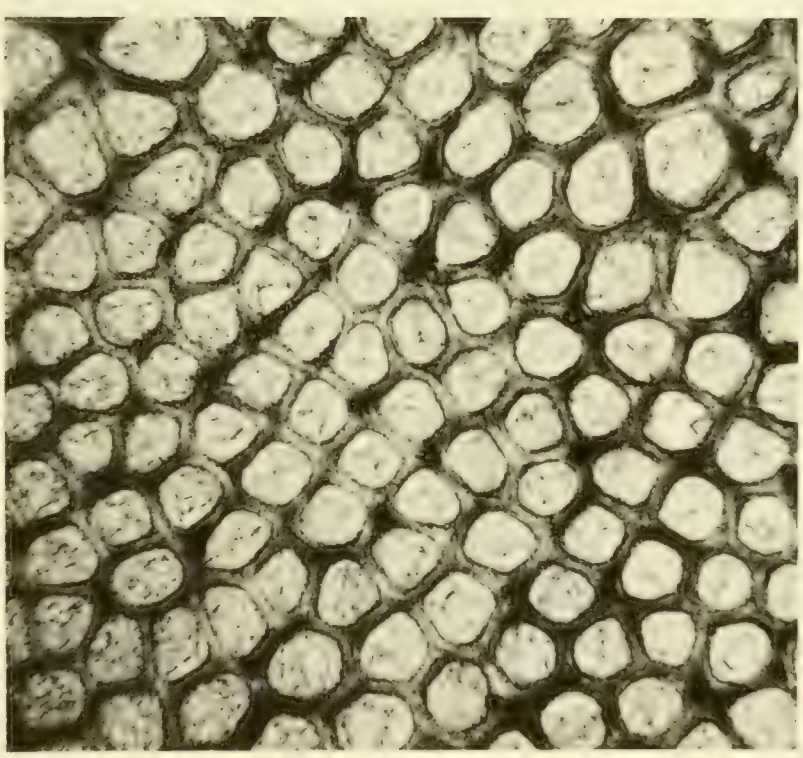

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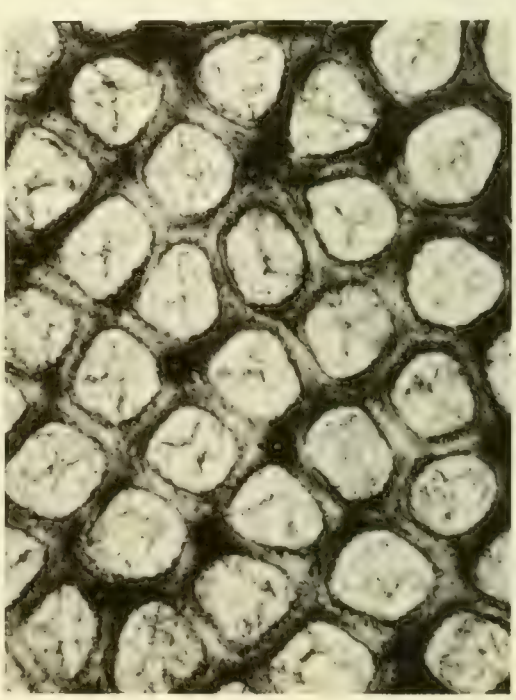

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PLATE 4

All figures are ×30 except fig. 6 (×50).

Figs. 1-6. Genus *Dekayia* ..... p. 71

1. YPM 25854, Loc. 203 (A-6304), longitudinal section.
2. YPM 25852, Loc. 132 (A-6440), tangential section.
3. YPM 25850, Loc. 128 (A-6436), tangential section, same specimen as pl. 3, fig. 4.
4. YPM 25851, Loc. 203 (A-6304), tangential section.
5. YPM 25853, Loc. 126 (A-6434), tangential section.
6. YPM 25853, similar to fig. 5 only higher magnification.

PLATE 5

All figures ×30.

Figs. 1-4. Genus *Dekayia* ..... p. 71

1. YPM 25852, Loc. 132 (A-6440), longitudinal section, same specimen as pl. 4, fig. 2.
2. YPM 25851, Loc. 203 (A-6304), longitudinal section, same specimen as pl. 4, fig. 4.
3. YPM 25855, Loc. 203 (A-6302), longitudinal section.
4. YPM 25856, Loc. 128 (A-6436), longitudinal section.

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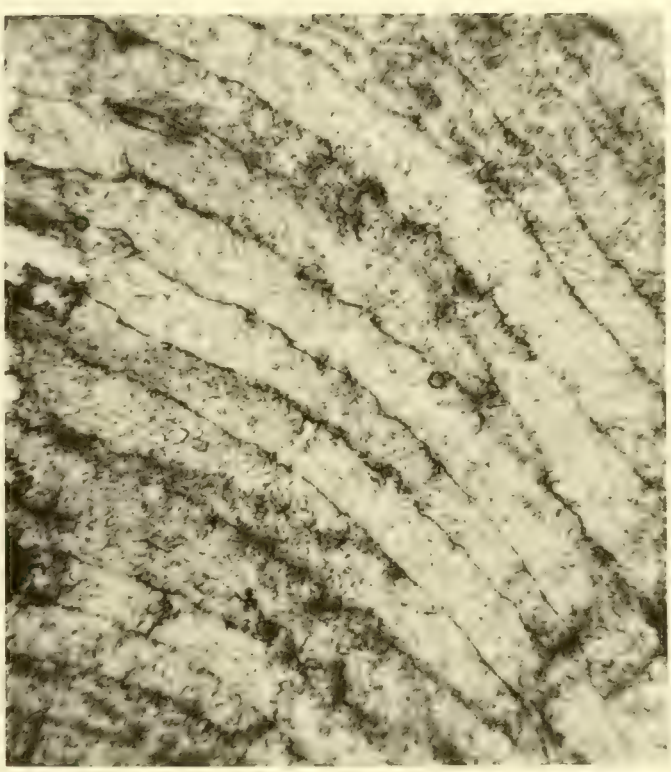

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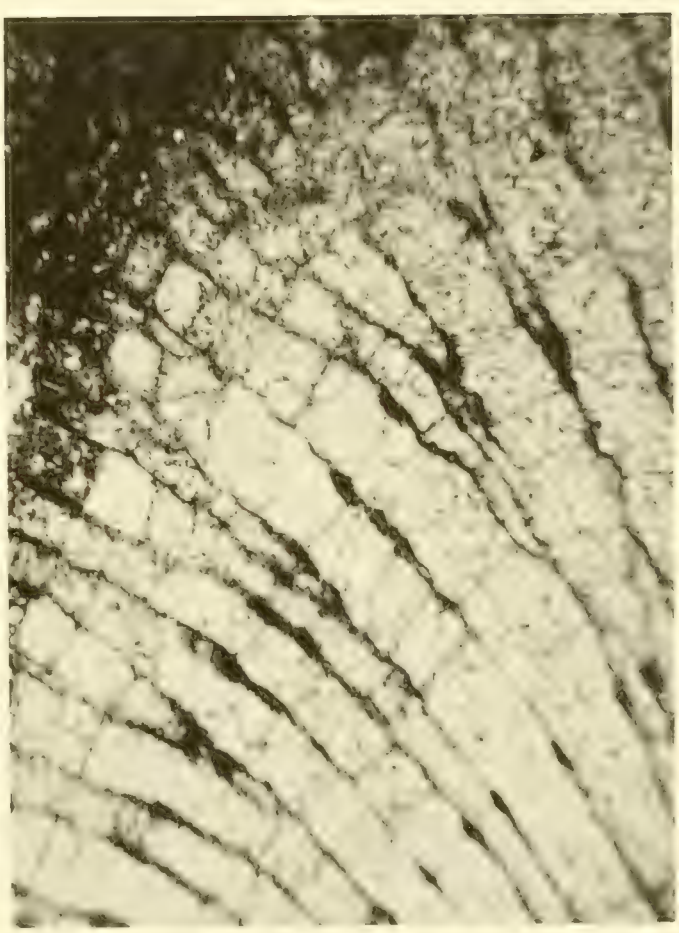

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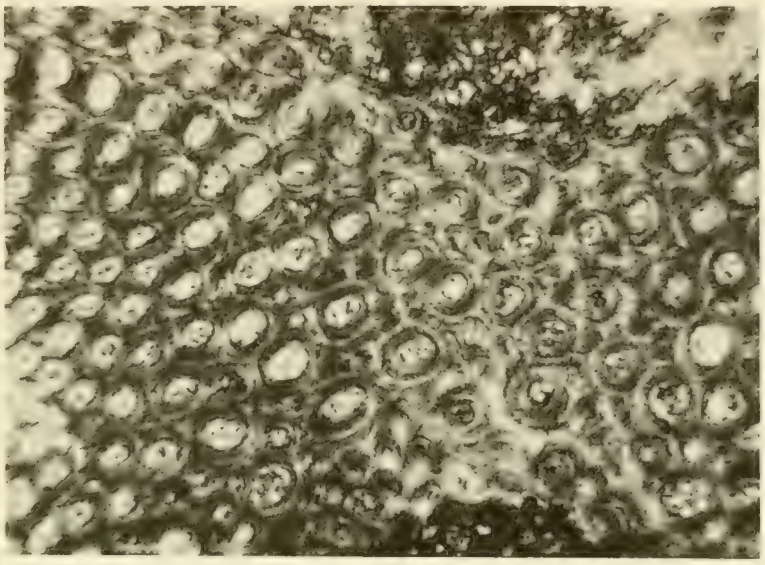

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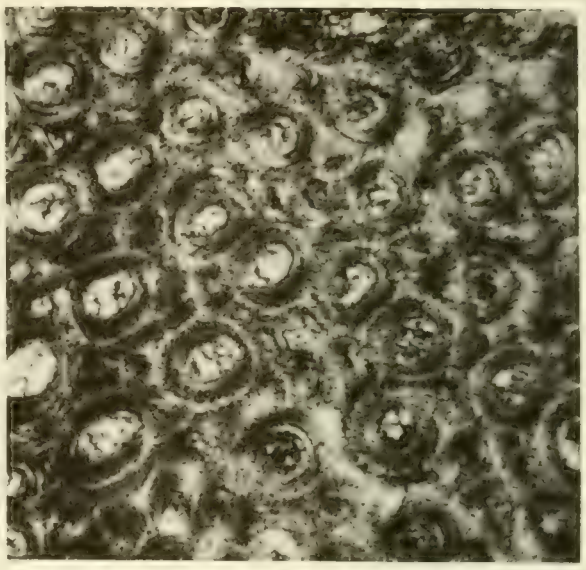

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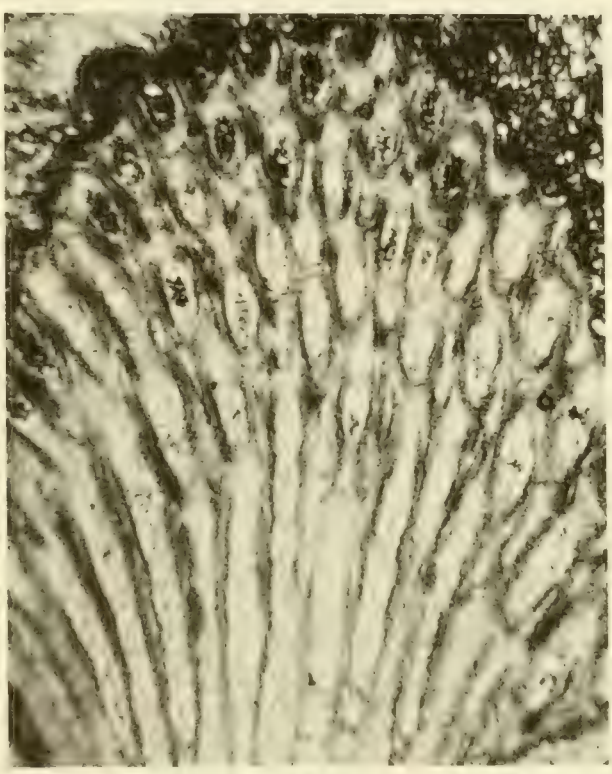

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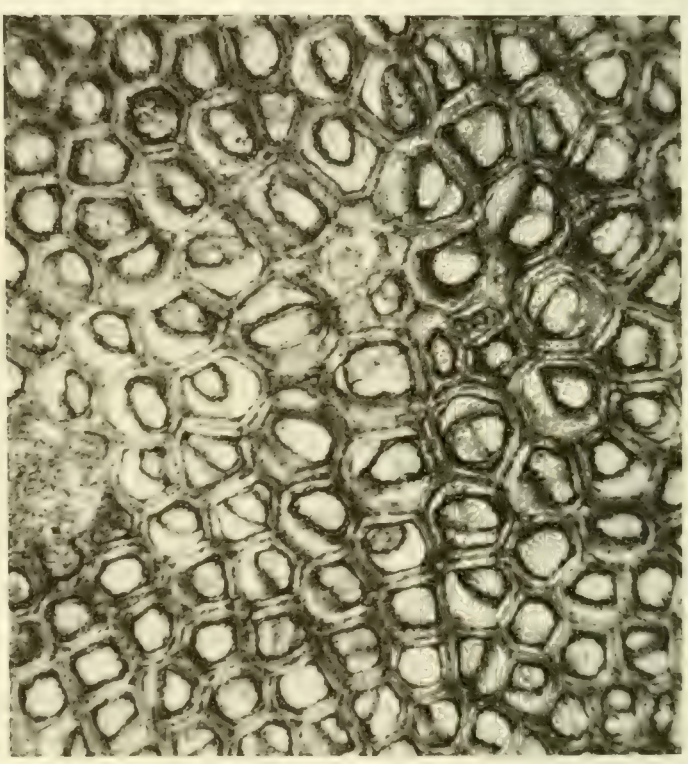

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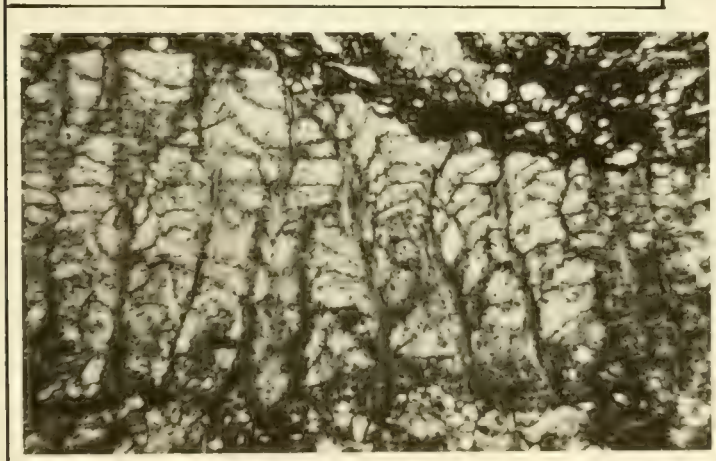

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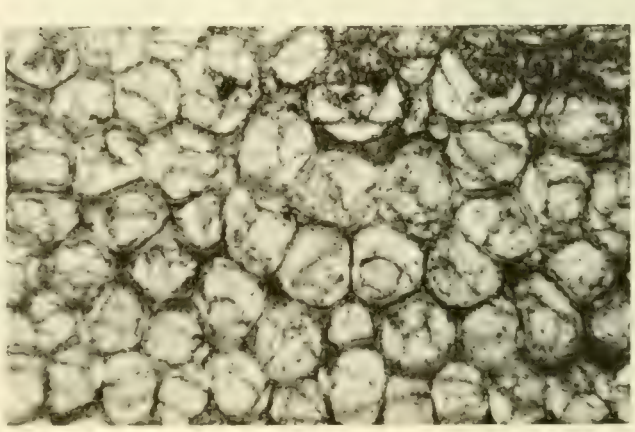

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PLATE 6

All figures are ×30 except fig. 2 (×50).

Figs. 1-3. Genus *Batostomella* ..... p. 73

1. YPM 25857, Loc. 126 (A-6434), tangential section.
2. YPM 25857, similar to fig. 1 only higher magnification.
3. YPM 25857, Loc. 126 (A-6434), longitudinal section, growing tip, same specimen as fig. 1.

Figs. 4-5. Genus *Peronopora* ..... p. 74

4. YPM 25858, Loc. 140 (A-6447), tangential.
5. YPM 25859, Loc. 125 (A-6443), longitudinal section.

Fig. 6. Probable Genus *Peronopora* ..... p. 74

6. YPM 25860, Loc. 141 (A-6448), tangential section.

PLATE 7

All figures are ×30 except fig. 1 (×50).

Figs. 1-2. Genus *Heterotrypa* ..... p. 74

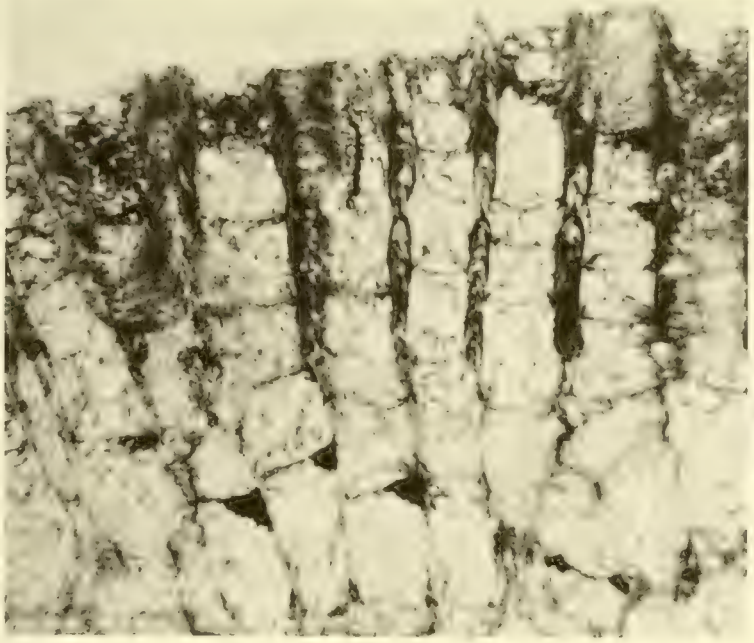
1. YPM 25861, Loc. 140 (A-6447), transverse section.
2. YPM 25862, Loc. 125 (A-6433), longitudinal? section of small fragmentary specimen.

Figs. 3, 5. Genus *Amplexopora* ..... p. 74

3. YPM 25863, Loc. 131 (A-6439), transverse section.
5. YPM 25863, Loc. 131 (A-6439), tangential section, same specimen as figure 3.

Figs. 4, 6. Probable Genus *Amplexopora* ..... p. 74

4. YPM 25864, Loc. 141 (A-6448), transverse section.
6. YPM 25865, Loc. 141 (A-6448), longitudinal section.



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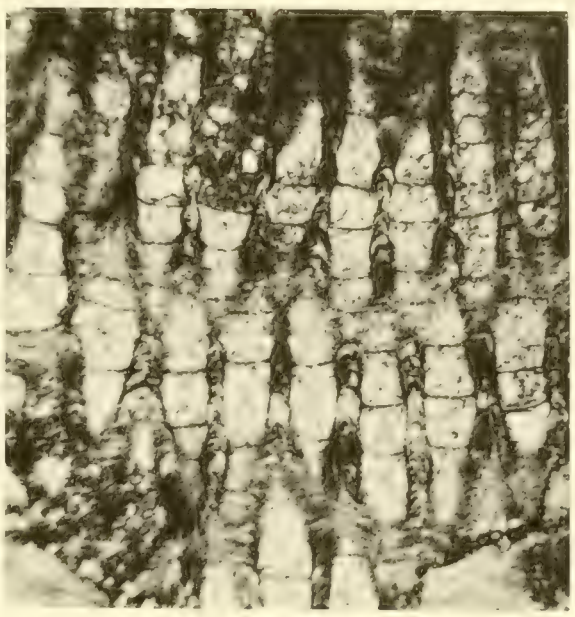

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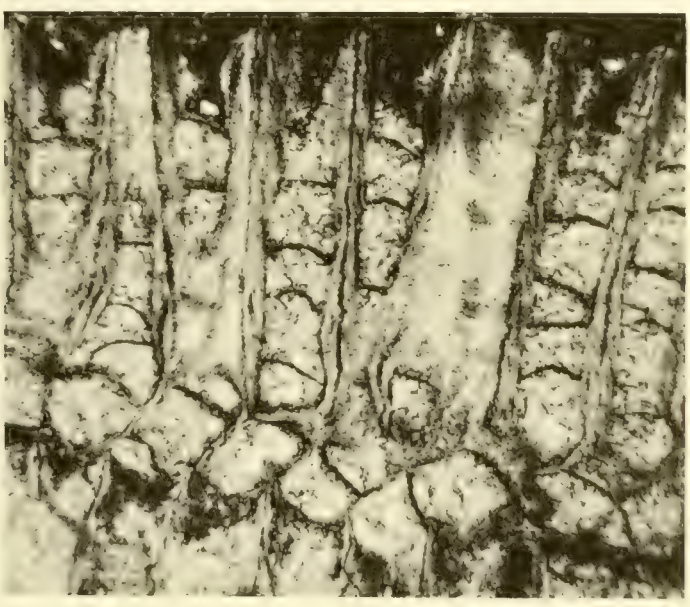

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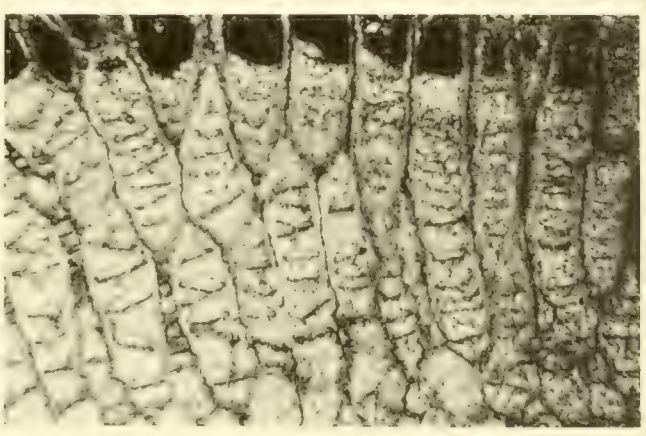

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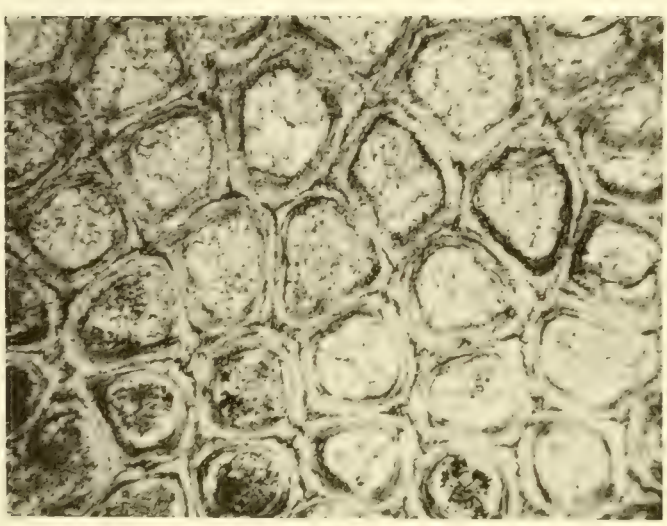

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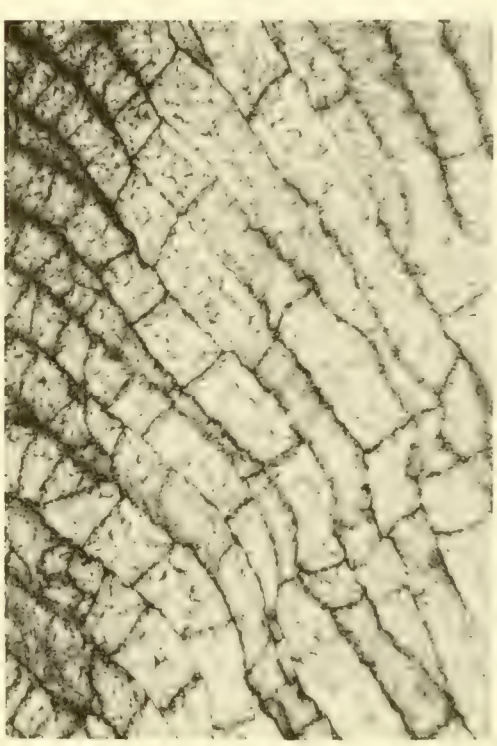

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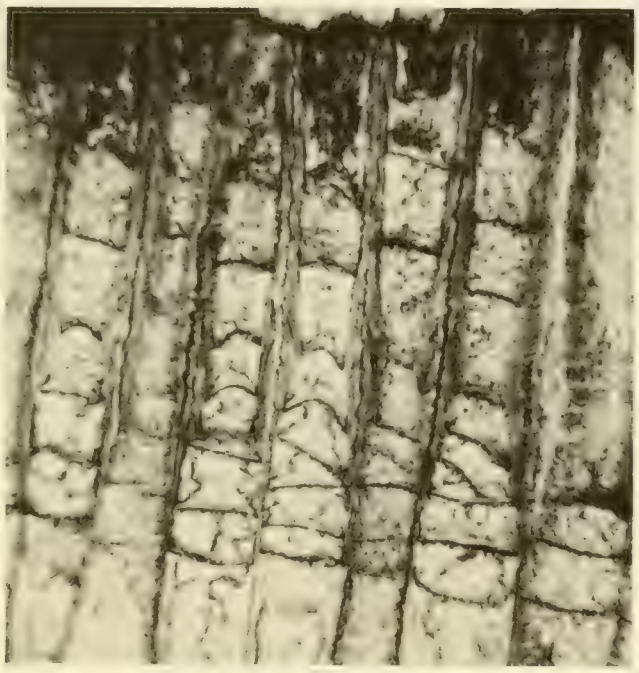

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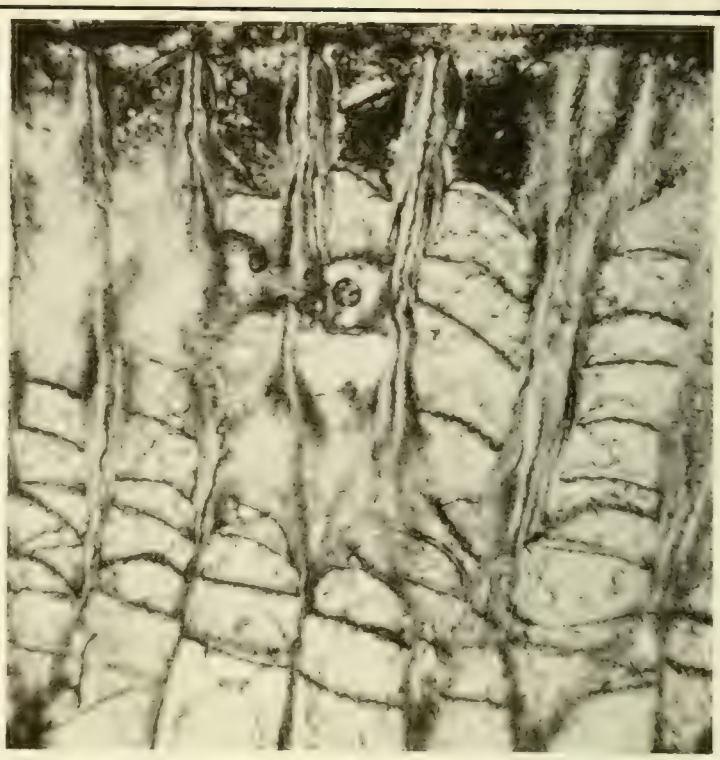

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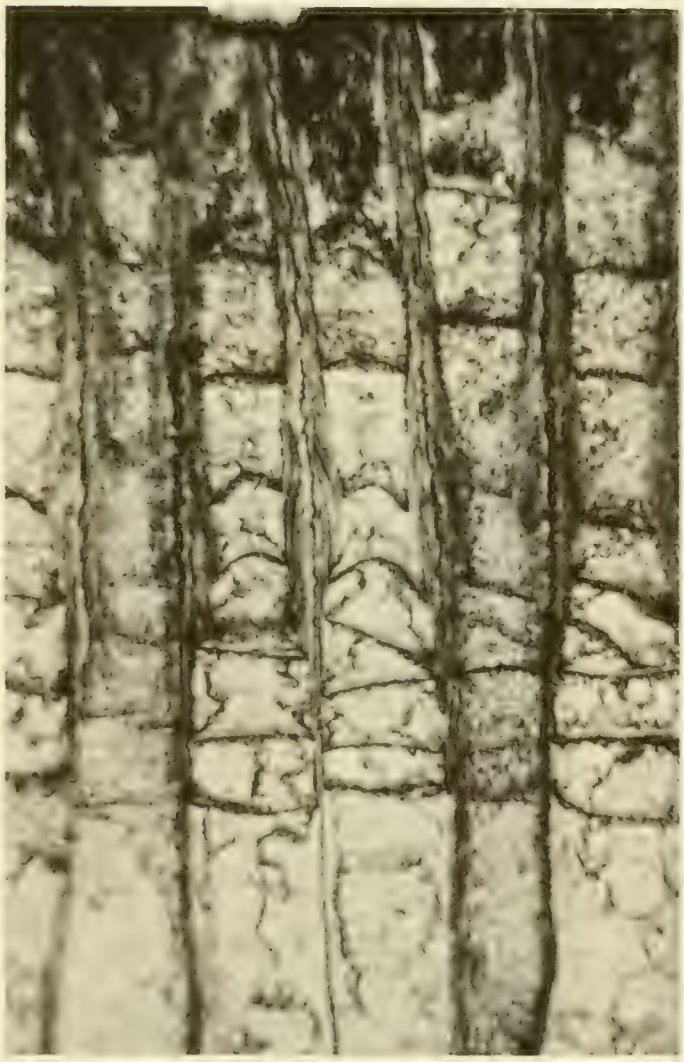

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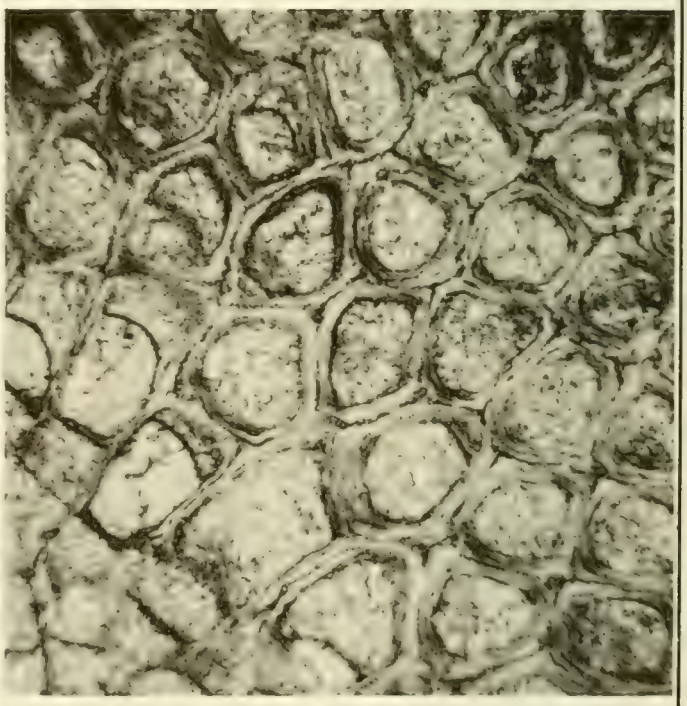

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PLATE 8

All figures are ×30 except fig. 3 (×50)

Figs. 1-4. Genus *Amplexopora* ..... p. 74

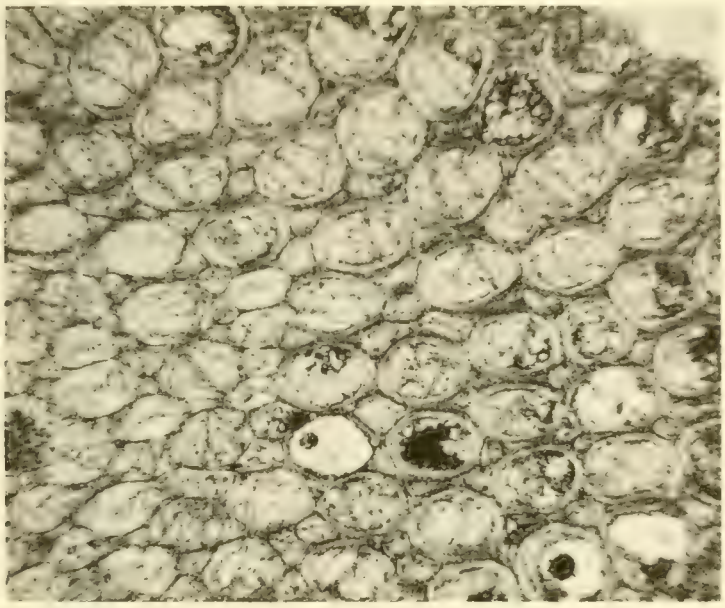
1. YPM 25866, Loc. 131 (A-6439), longitudinal section.
2. YPM 25866, Loc. 131 (A-6439), longitudinal section, same specimen as fig. 1.
3. YPM 25866, similar to fig. 1 only higher magnification.
4. YPM 25863, Loc. 131 (A-6439), tangential section, same specimen as pl. 7, fig. 3.

PLATE 9

All figures are ×30 except fig. 5 (×50).

Figs. 1-6. Genus *Hallopora* ..... p. 75

1. YPM 25867, Loc. 127 (A-6435), tangential section.
2. YPM 25868, Loc. 34-A (A-6345), tangential section.
3. YPM 25869, Loc. 147 (A-6453), longitudinal section.
4. YPM 25867, Loc. 127 (A-6435), longitudinal section, same specimen as fig. 1.
5. YPM 25870, Loc. 34-A (A-6345), transverse section.
6. YPM 25871, Loc. 147 (A-6453), tangential section.



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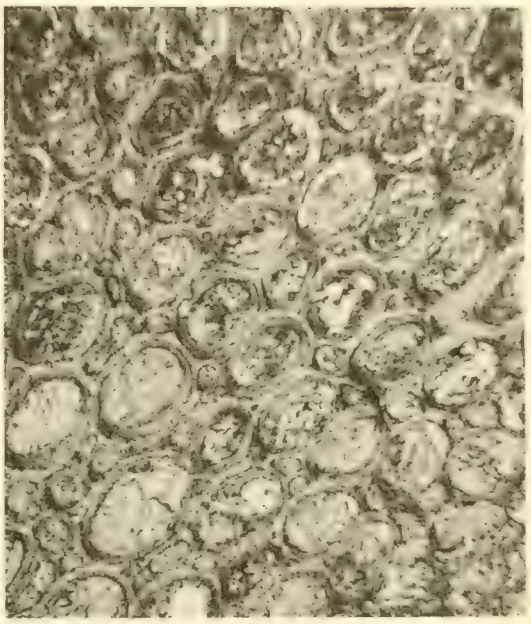

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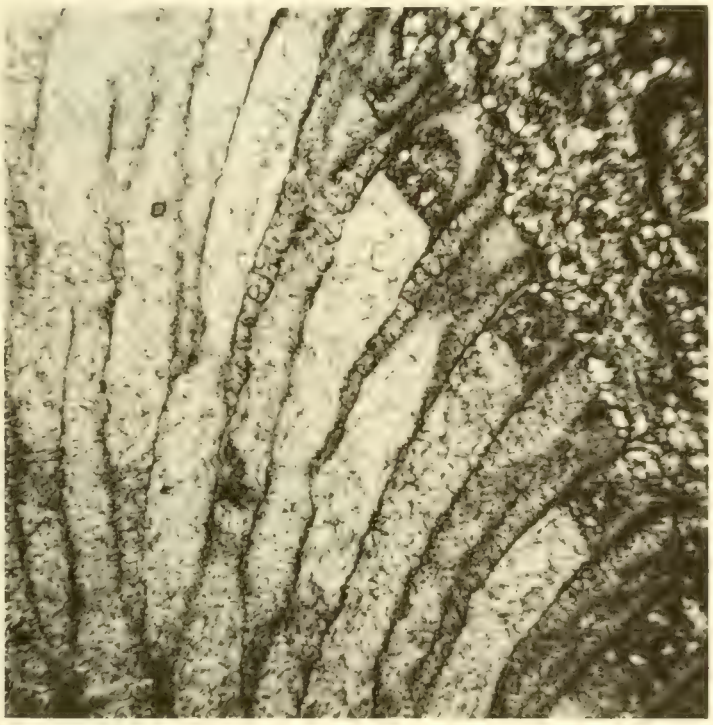

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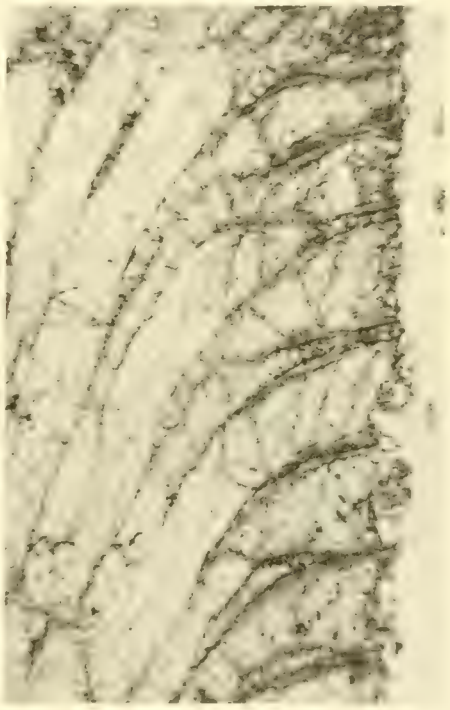

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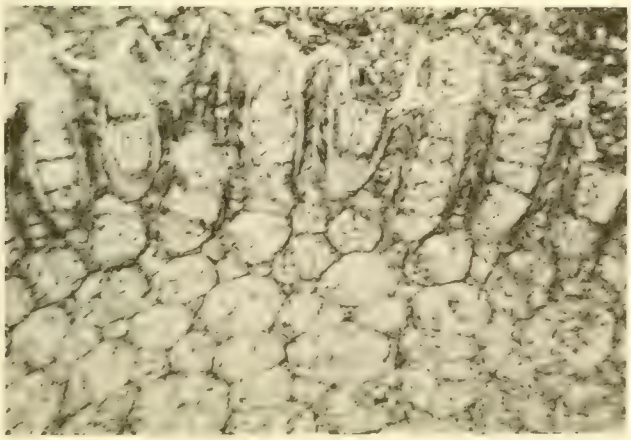

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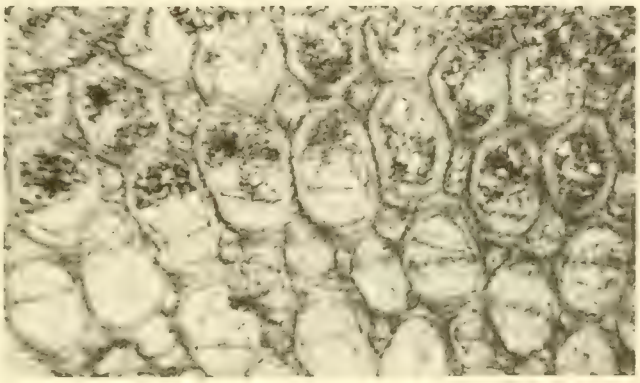

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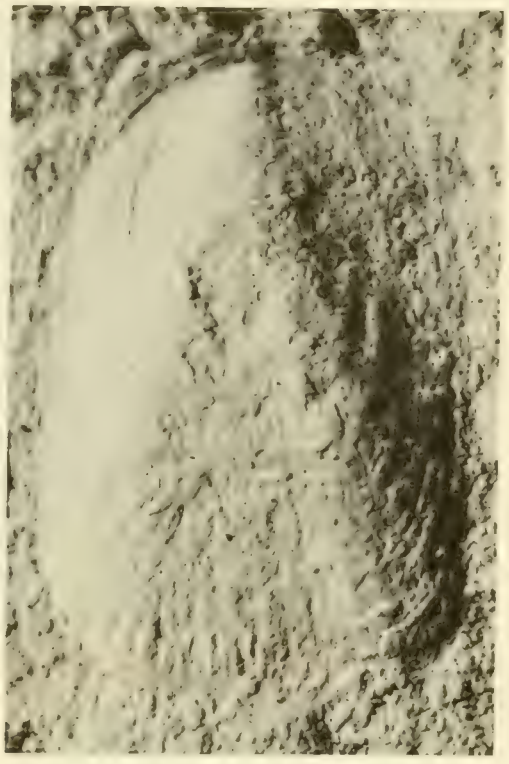

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PLATE 10

All figures are ×4.

Figs. 1-5. Genus *Lingula*? ..... p. 76

1. YPM 25872, Loc. 98 (A-6414).
2. YPM 25873, Loc. 203 (A-6309).
3. YPM 25874, Loc. 179 (A-6478).
4. YPM 25875, Loc. 203 (A-6314).
5. YPM 25876, Loc. 203 (A-6309).

PLATE 11

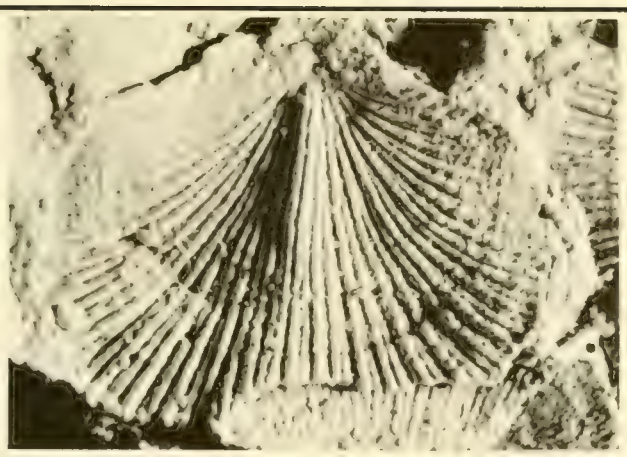
All figures are ×4 except figs. 7, 8 (×2).

Figs. 1-6. *Onniella multisecta* (Meek) ..... p. 82

1. YPM 25877, Loc. 35 (G) (A-6352), brachial valve external. Image reversed.
2. YPM 25878, Loc. 39 (A-6365), pedicle valve internal, latex impression of fig. 5, showing large hinge teeth and deeply impressed crural fossettes.
3. YPM 25879, Loc. 35 (B) (A-6347), brachial valve internal, latex impression of fig. 4.
4. YPM 25879, Loc. 35 (B) (A-6347), brachial valve internal mold (natural).
5. YPM 25878, Loc. 39 (A-6365), pedicle valve internal mold (natural).
6. YPM 25880, Loc. 39 (A-6365), brachial valve internal mold (natural).

Figs. 7-8. *Hebertella sinuata* (Hall) ..... p. 78

7. YPM 25881, Loc. 147 (A-6453), pedicle valve internal mold (natural).
8. YPM 25882, Loc. 147 (A-6453), brachial valve internal mold (natural).



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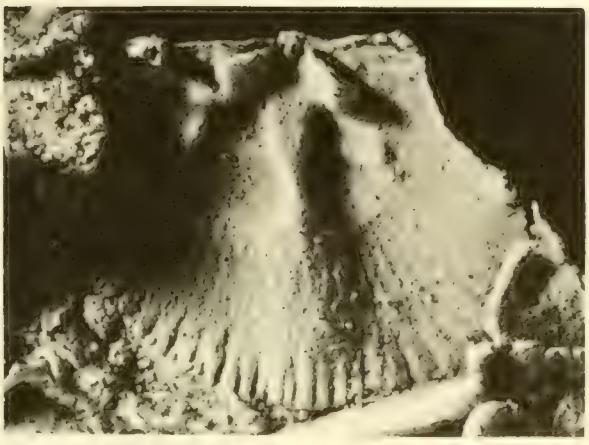

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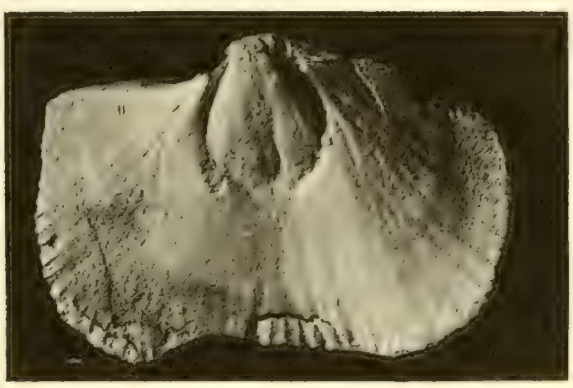

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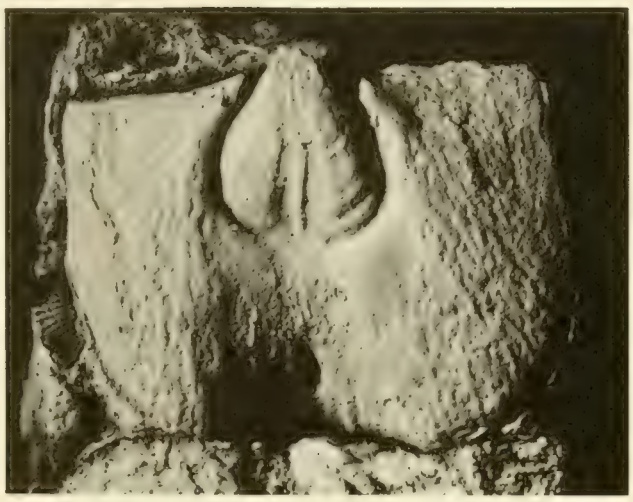

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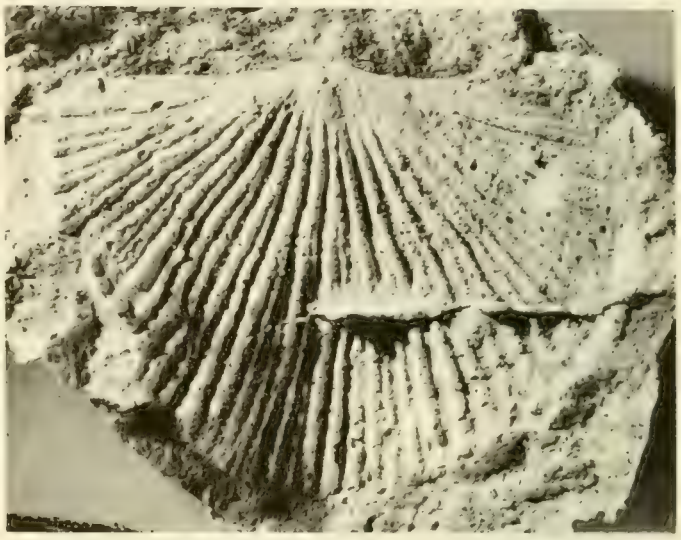

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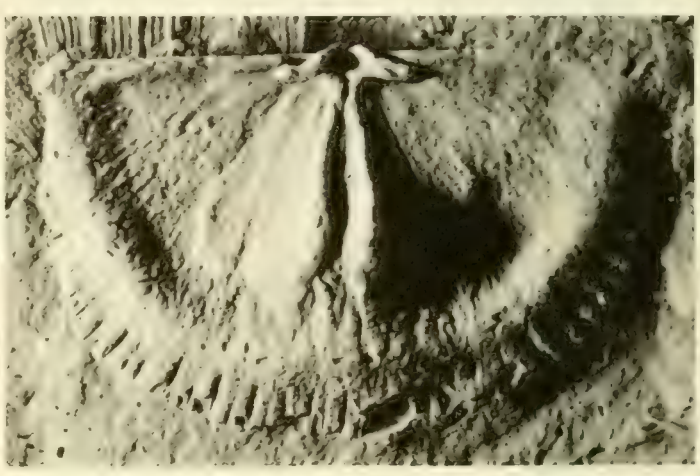

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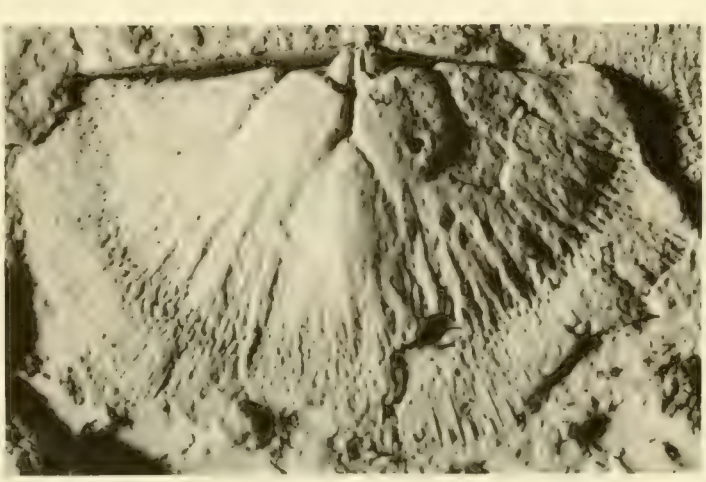

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PLATE 12

All figures are ×4 except figs. 1, 2 (×2).

Fig. 1. *Hebertella sinuata* (Hall) ..... p. 78

1. YPM 25883, Loc. 147 (A-6453), pedicle valve internal mold (natural).

Fig. 2. Probable *Hebertella sinuata* (Hall) ..... p. 78

2. YPM 25884, Loc. 15 (A-6330), ?brachial valve external, latex impression.

Figs. 3-6. *Sowerbyella* (*Sowerbyella*) *sericea* (Hall) ..... p. 85

3. YPM 25885, Loc. 31 (A-6341), brachial valve internal mold (natural).
4. YPM 25886, Loc. 31 (A-6341), brachial valve internal, latex impression showing well-defined submedial septa and curved crural bases.
5. YPM 25887, Loc. 31 (A-6341), pedicle valve internal mold (natural) showing well-defined ventral muscle scars.
6. YPM 25888, Loc. 31 (A-6341), pedicle valve external, latex impression.

PLATE 13

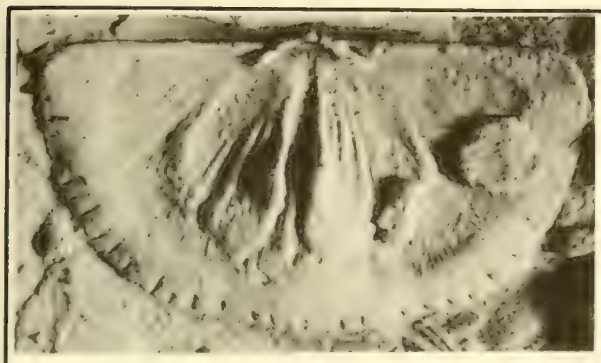
Figures 1-4 (×4), Figures 5-8 (×2).

Figs. 1-4. *Sowerbyella (Sowerbyella) sericea* (Hall) ..... p. 85

1. YPM 25889, Loc. 31 (A-6341), brachial valve internal, latex impression showing flat-lying submedial septa flanking median septum. Lighting from lower right.
2. YPM 25890, Loc. 31 (A-6341), pedicle valve internal mold (natural) showing well-defined ventral muscle scars.
3. YPM 25891, Loc. 31 (A-6341), brachial valve external.
4. YPM 25892, Loc. 31 (A-6341), brachial valve internal mold (natural).

Figs. 5-8. *Orthorhynchula linneyi* (James) ..... p. 91

5. YPM 25893, Loc. 203 (A-6303), brachial valve up.
6. YPM 25894, Loc. 203 (A-6307), posterior internal latex impression showing prominent crura in brachial valve; impression of fig. 7.
7. YPM 25894, Loc. 203 (A-6307), internal mold (natural), umbo very prominent.
8. YPM 25895, Loc. 203 (A-6306), internal mold (natural).



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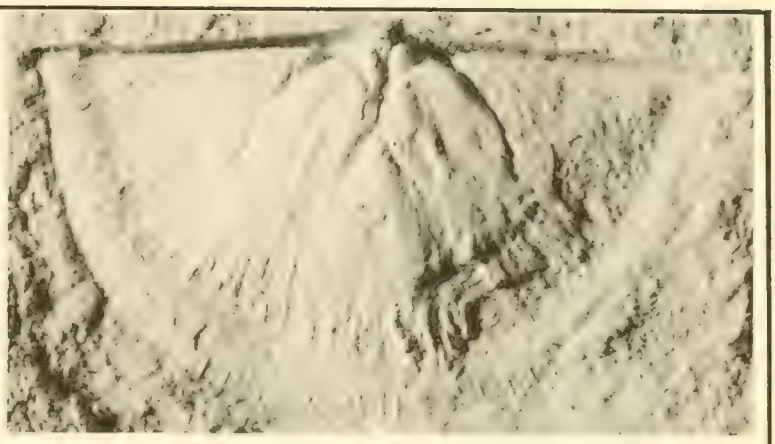

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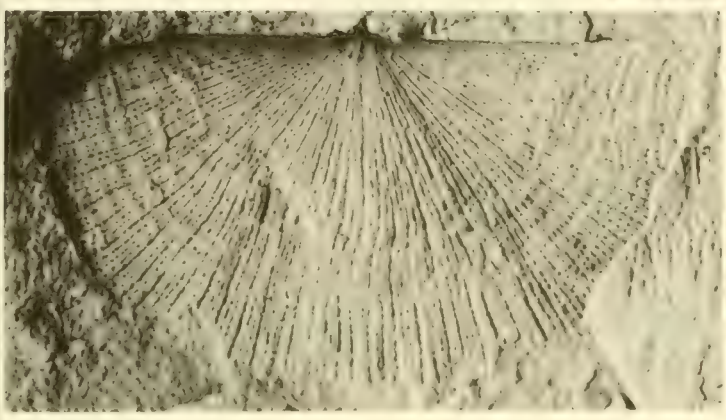

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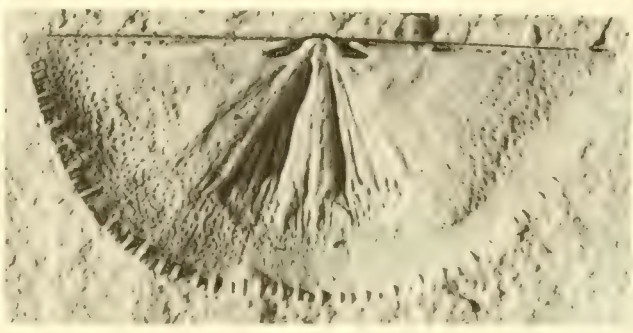

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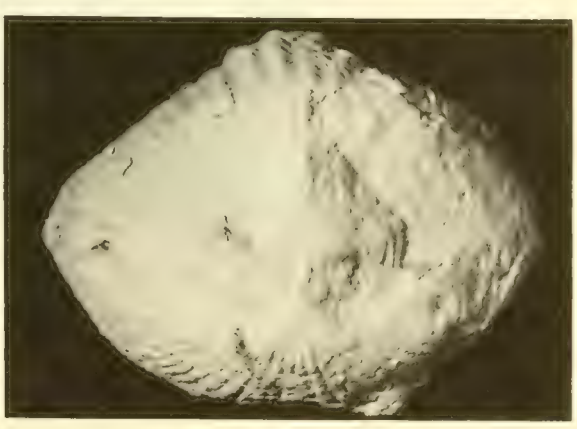

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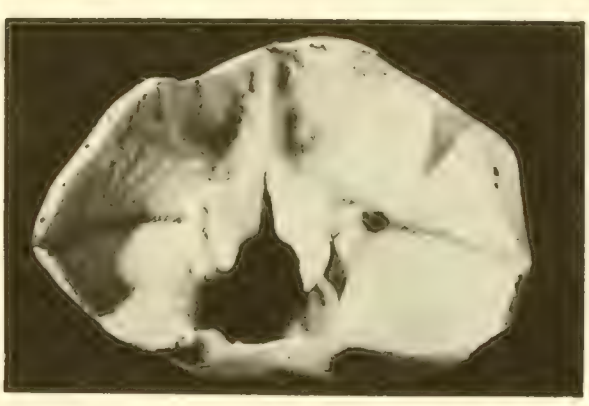

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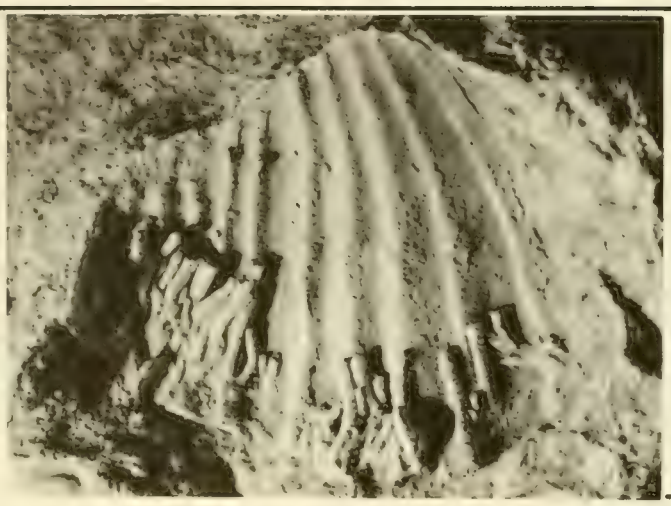

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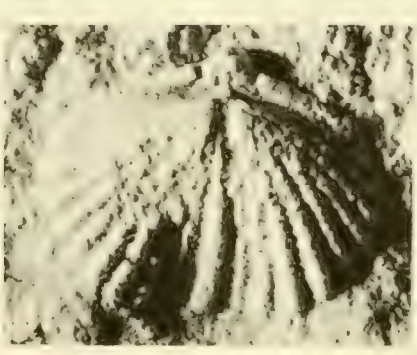

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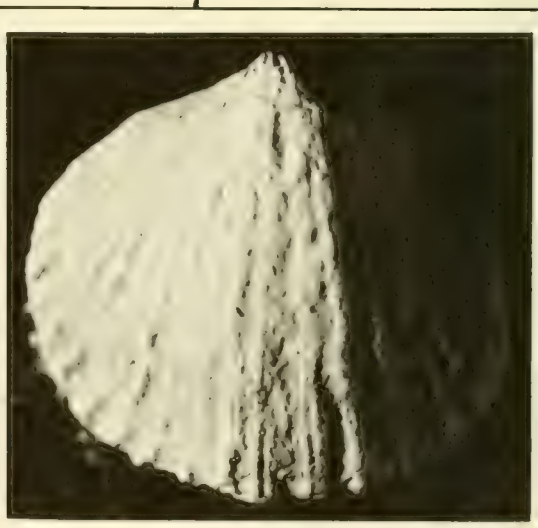

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PLATE 14

Figures 1-5 (×2), Figures 6-9 (×4).

Figs. 1-5. *Orthorhynchula linneyi* (James) ..... p. 91

1. YPM 25896, Loc. 203 (A-6308), external mold (natural), concentration of worm tubes along anterior inhalent margins. Image reversed.
2. YPM 25897, Loc. 203 (A-6303), brachial valve up.
3. YPM 25898, Loc. 203 (A-6307), internal mold (natural) pedicle valve up.
4. YPM 25899, Loc. 203 (A-6308), latex impression of external mold showing small worm tubes covering surface of valve; tubes concentrated along each radial interspace.
5. YPM 25900, Loc. 185 (A-6484), pedicle valve left.

Figs. 6-7. *Zygospira modesta* (Hall) ..... p. 96

6. YPM 25901, Loc. 110 (A-6425).
7. YPM 25902, Loc. 110 (A-6425).

Figs. 8-9. *Zygospira recurvirostra* (Hall) ..... p. 98

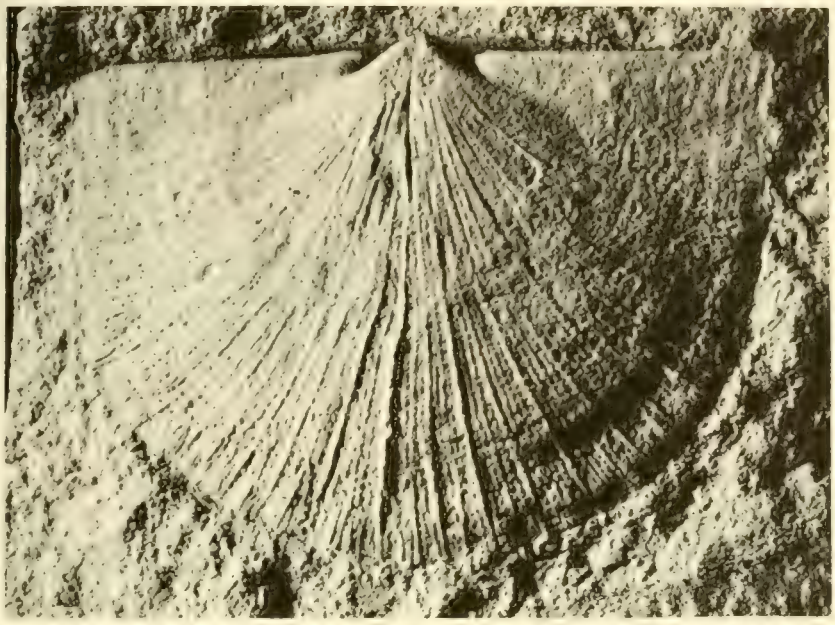
8. YPM 25903, Loc. 141 (A-6448).
9. YPM 25904, Loc. 141 (A-6448).

PLATE 15

All figures are ×2.

Figs. 1-6. *Rafinesquina* "*alternata*" (Hall) ..... p. 87

1. YPM 25905, Loc. 37 (4) (A-6363), pedicle valve internal mold (natural).
2. YPM 25906, Loc. 31 (A-6341), pedicle valve external.
3. YPM 25907, Loc. 31 (A-6341), pedicle valve external.
4. YPM 25908, Loc. 98 (1) (A-6414), pedicle valve internal mold (natural).
5. YPM 25909, Loc. 183 (A-6482), pedicle valve internal mold (natural).
6. YPM 25910, Loc. 49 (A-6376), pedicle valve internal mold (natural).



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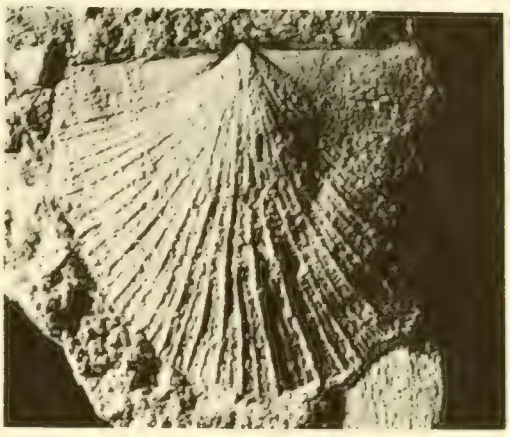

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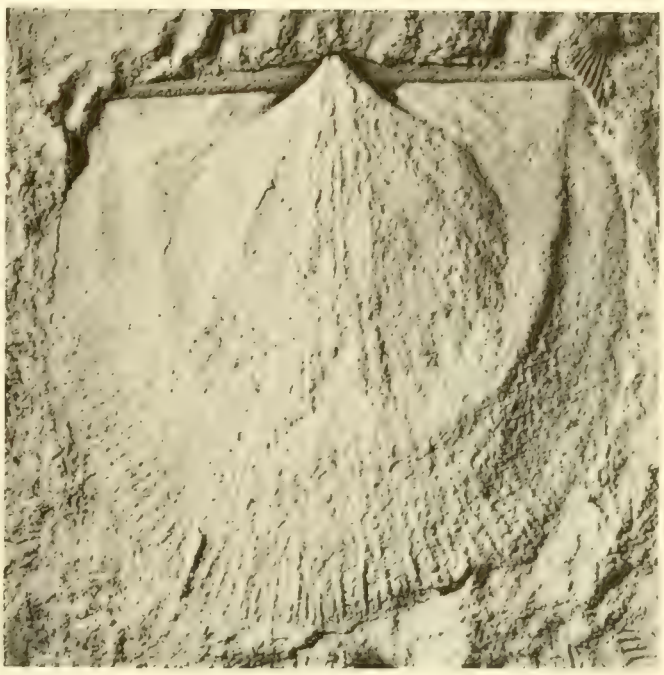

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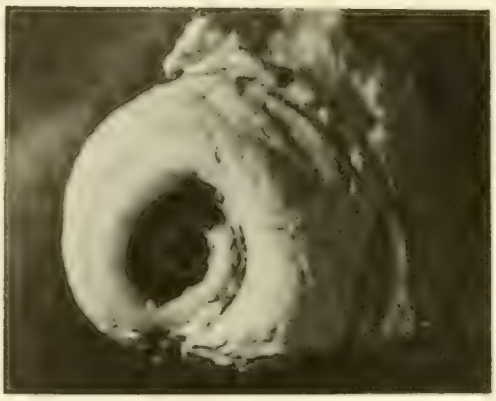

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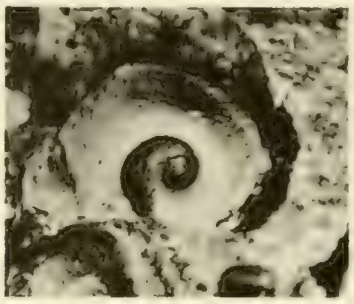

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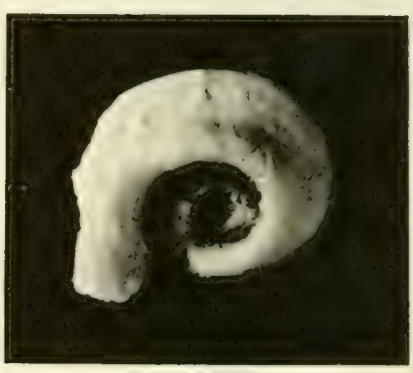

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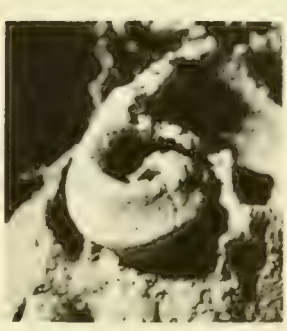

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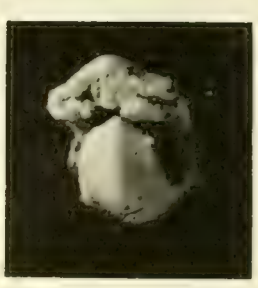

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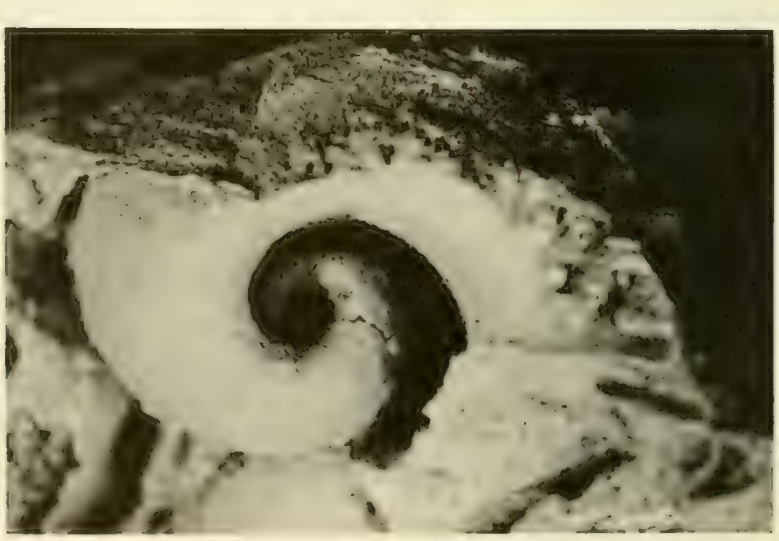

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PLATE 16

All figures are ×4.

Figs. 1-9. *Plectonotus*? sp. ..... p. 101

1. YPM 25911, Loc. 203 (A-6316).
2. YPM 25912, Loc. 203 (A-6310).
3. YPM 25911, Loc. 203, (A-6316), latex impression of the external mold of fig. 1.
4. YPM 25913, Loc. 148 (A-6454).
5. YPM 25914, Loc. 203 (A-6316).
6. YPM 25915, Loc. 203 (A-6316). Specimen lost.
7. YPM 25916, Loc. 203 (A-6308).
8. YPM 25917, Loc. 203 (A-6316).
9. YPM 25918, Loc. 203 (A-6316).

Figs. 10-11. *Bucania* sp. ..... p. 102

10. YPM 25919, Loc. 87 (A-6404).
11. YPM 25920, Loc. 87 (A-6404).

PLATE 17

All figures are ×4 except fig. 2 (×2).

Figs. 1-3. *Bucania* sp. ..... p. 102
1. YPM 25921, Loc. 203 (A-6303).
2. YPM 25922, Loc. 87 (A-6404).
3. YPM 25923, Loc. 87 (A-6404).

Figs. 4. Genus *Seelya* ..... p. 105
4. YPM 25924, Loc. 167 (A-6467).

Figs. 5. Genus *Cyclonema* ..... p. 106
5. YPM 25925, Loc. 75 (A-6395).

Figs. 6. Genus *Trochonema* ..... p. 110
6. YPM 25926, Loc. 101 (4) (A-6417).

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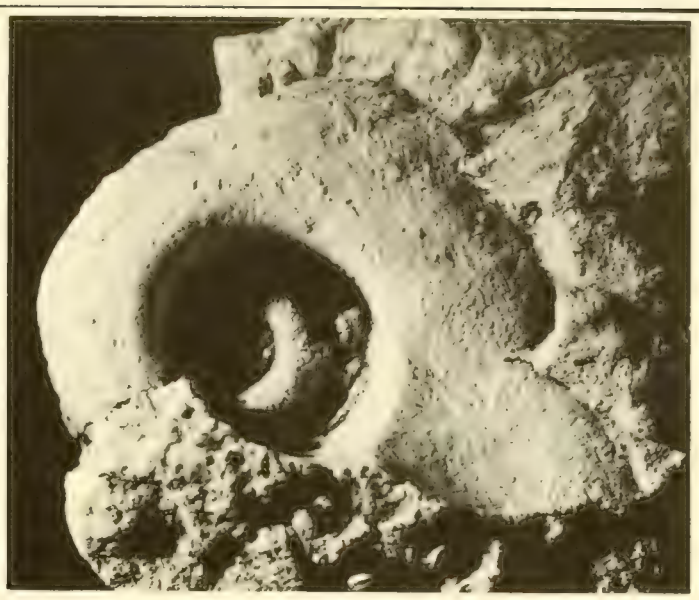

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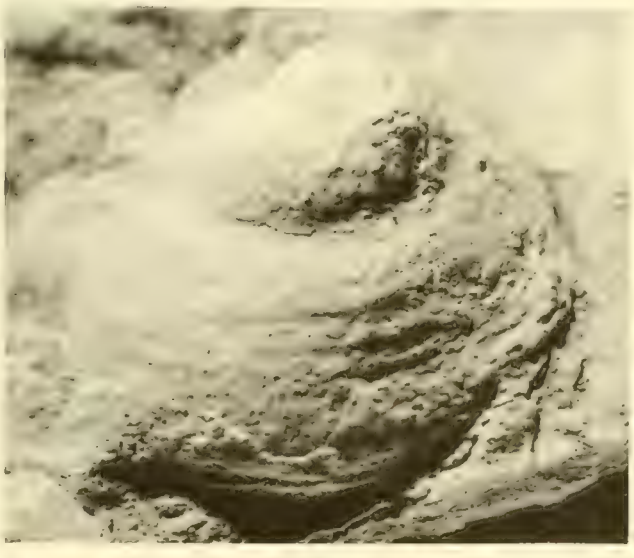

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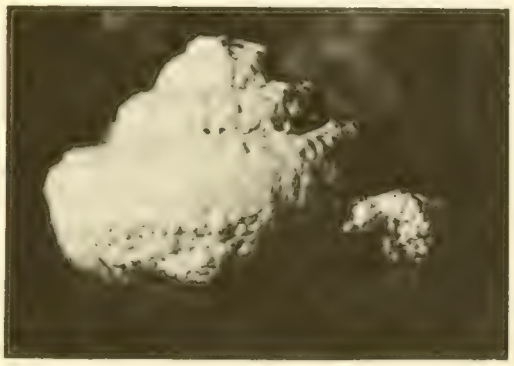

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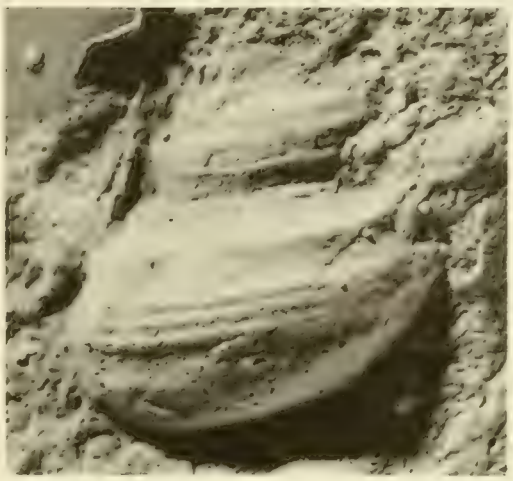

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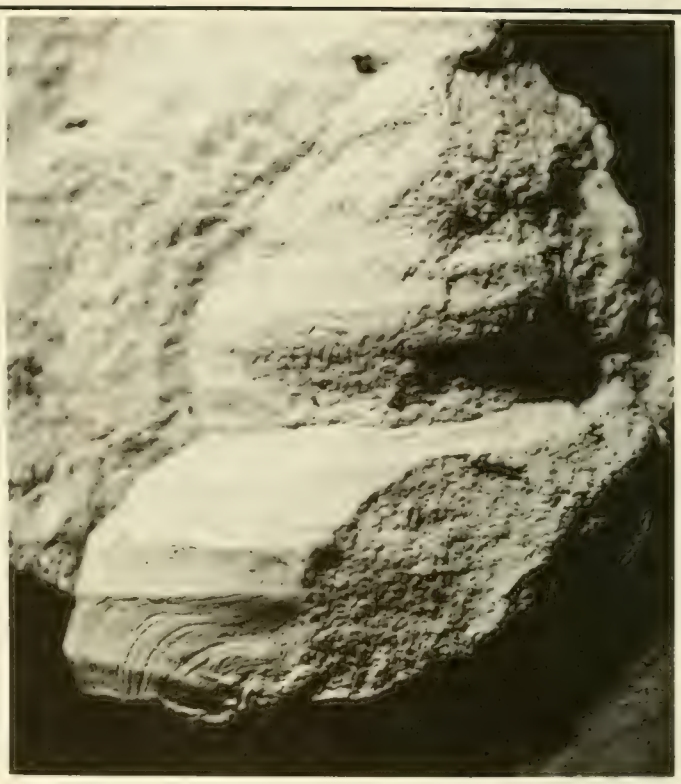

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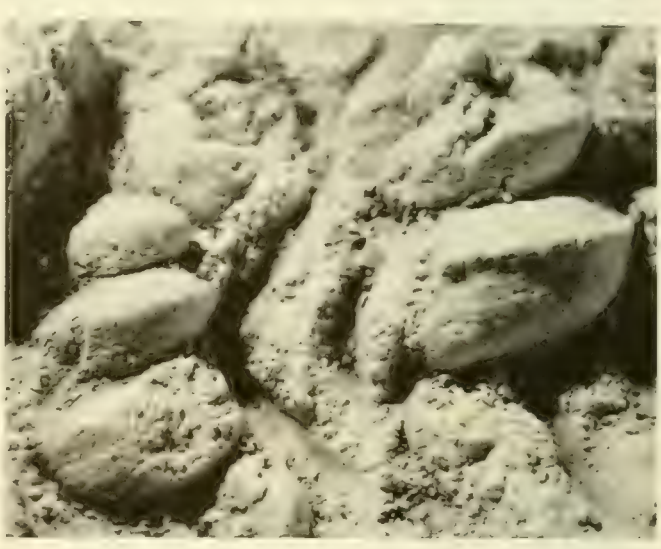

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PLATE 18

All figures are ×4.

Figs. 1-2. *Ruedemannia? lirata* (Ulrich & Scofield) ..... p. 104

1. YPM 25927, Loc. 50 (A-6377), latex impression showing pronounced trilineate banding.
2. YPM 25928, Loc. 34-A (A-6345), bilineate banding and fine growth lines well-preserved.

Fig. 3. *Loxoplocus* (*Lophospira*) *ventricosta* (Hall) ..... p. 108

3. YPM 25929, Loc. 167 (A-6467), latex impression.

Figs. 4-6. *Loxoplocus* (*Lophospira*) *abbreviata* (Hall) ..... p. 106

4. (right) — YPM 25931, Loc. 179 (A-6478).
5. YPM 25932, Loc. 167 (A-6467).
6. YPM 25933, Loc. 203 (A-6316).

Figs. 4, 7. *Loxoplocus* (*Lophospira*) *perangulata* (Hall) ..... p. 109

4. (left) — YPM 25930, Loc. 179 (A-6478).
7. YPM 25934, Loc. 179 (A-6478).

PLATE 19

All figures are ×4 except fig. 3 (×2).

Figs. 1-2. Genus *Sinuopea*? ..... p. 110

1. YPM 25935, Loc. 167 (A-6467).
2. YPM 25936, Loc. 167 (A-6467), latex impression.

Figs. 3-4. Genus *Murchisonia*? ..... p. 111

3. YPM 25937, Loc. 133 (A-6441).
4. YPM 25938, Loc. 133 (A-6441).

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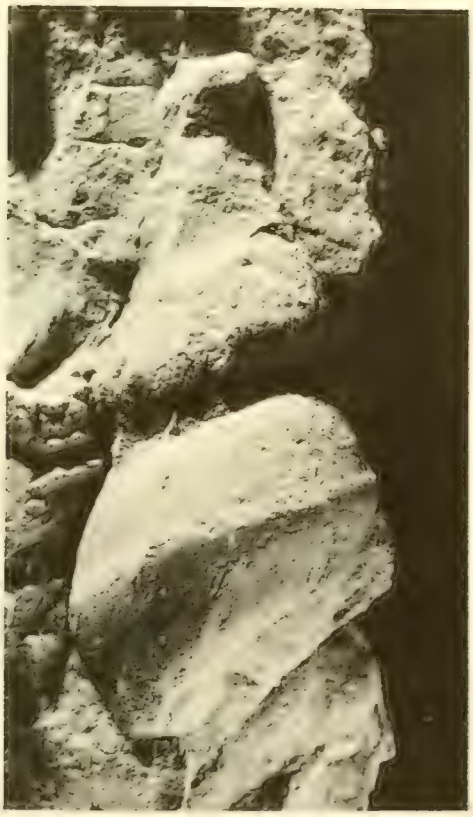

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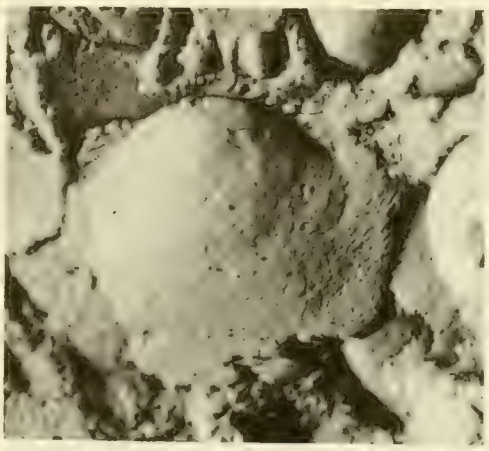

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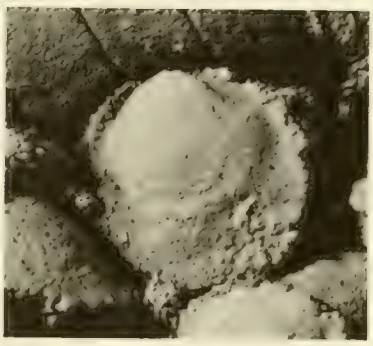

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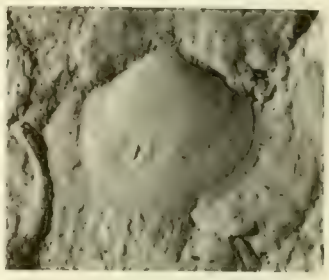

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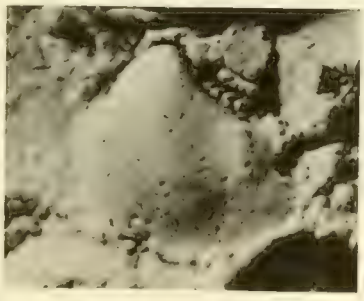

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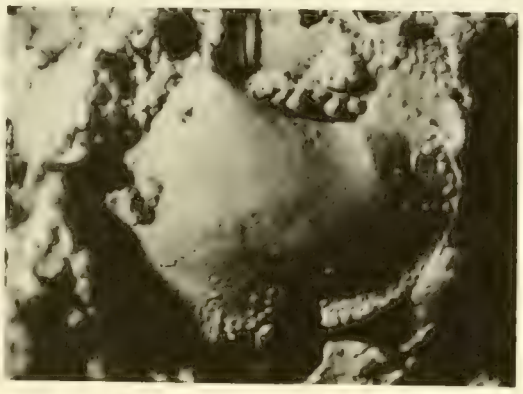

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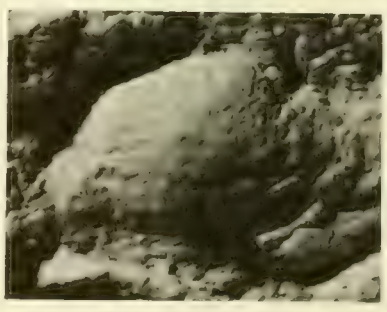

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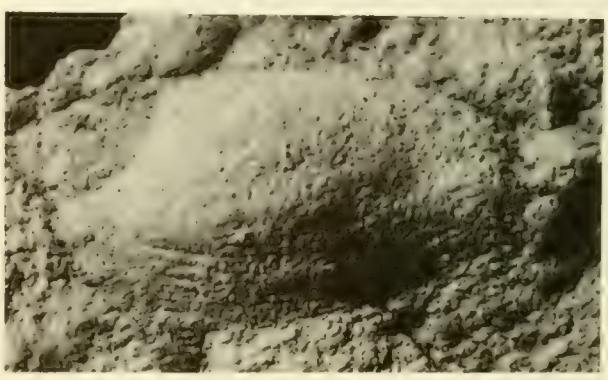

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PLATE 20

All figures are ×4.

Figs. 1-3. *Ctenodonta? pulchella* (Hall) ..... p. 112

1. YPM 25939, Loc. 37 (A-6359).
2. YPM 25940, Loc. 37 (A-6359).
3. YPM 25941, Loc. 37 (A-6359).

Fig. 4. Probable *Ctenodonta? pulchella* (Hall) ..... p. 112

4. YPM 25942, Loc. 34 (A) (A-6345).

Figs. 5-8. *Praenucula levata* (Hall) ..... p. 114

5. YPM 25943, Loc. 37 (A-6359).
6. YPM 25944, Loc. 97 (11) (A-6413).
7. YPM 25945, Loc. 77-A (A-6397).
8. YPM 25946, Loc. 37 (A-6359).

Figs. 9-11. Probable Genus *Palaeoneilo* ..... p. 114

9. YPM 25947, Loc. 135 (A-6443).
10. YPM 25948, Loc. 135 (A-6443).
11. YPM 25949, Loc. 148 (A-6454).

PLATE 21

All figures are ×4.

Figs. 1-7. *Tancrediopsis cuneata* (Hall) ..... p. 113

1. YPM 25950, Loc. 203 (A-6316).
2. YPM 25951, Loc. 203 (A-6317).
3. YPM 25952, Loc. 203 (A-6316).
4. YPM 25953, Loc. 84 (A-6402).
5. YPM 25954, Loc. 75 (A-6395).
6. YPM 25955, Loc. 82 (A-6400).
7. YPM 25956, Loc. 82 (A-6400).

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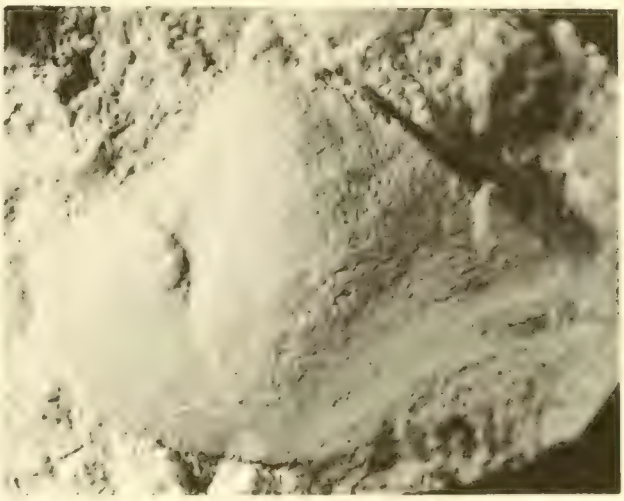

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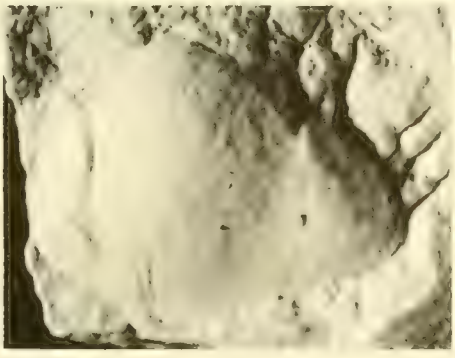

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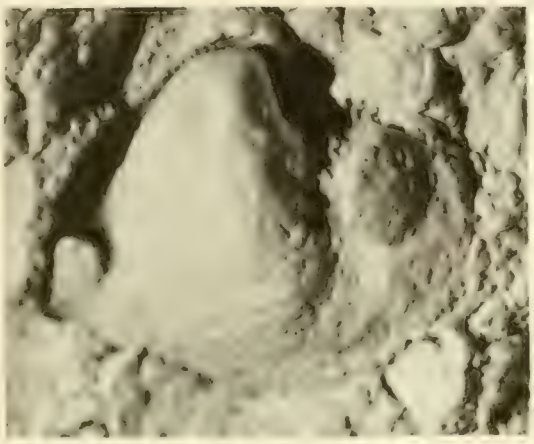

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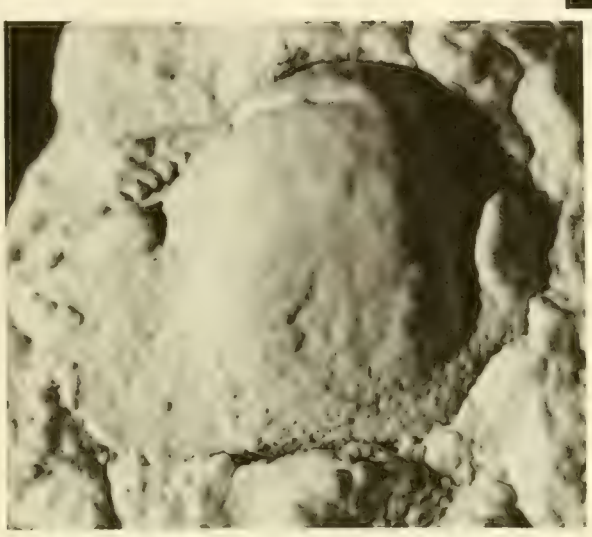

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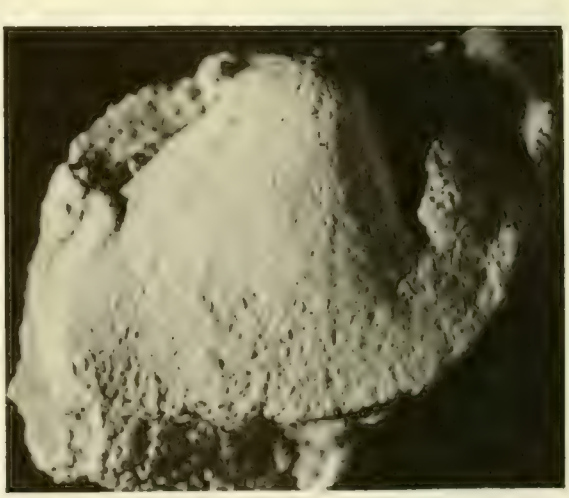

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PLATE 22

All figures are ×4.

Figs. 1-6. *Tancrediopsis cuneata* (Hall) ..... p. 113

1. YPM 25957, Loc. 203 (A-6309).
2. YPM 25958, Loc. 188 (A-6486).
3. YPM 25959, Loc. 203 (A-6308).
4. YPM 25960, Loc. 203 (A-6304).
5. YPM 25961, Loc. 201 (A-6497).
6. YPM 25962, Loc. 193 (A-6490).

PLATE 23

All figures are ×4.

Figs. 1-5. *Tancrediopsis cuneata* (Hall) ..... p. 113

1. YPM 25963, Loc. 203 (A-6313).
2. YPM 25964, Loc. 200 (A-6496).
3. (right) — YPM 25966, Loc. 203 (A-6316).
   (left) — YPM 25965, Loc. 203 (A-6316).
4. YPM 25967, Loc. 203 (A-6316).
5. YPM 25968, Loc. 203 (A-6316).

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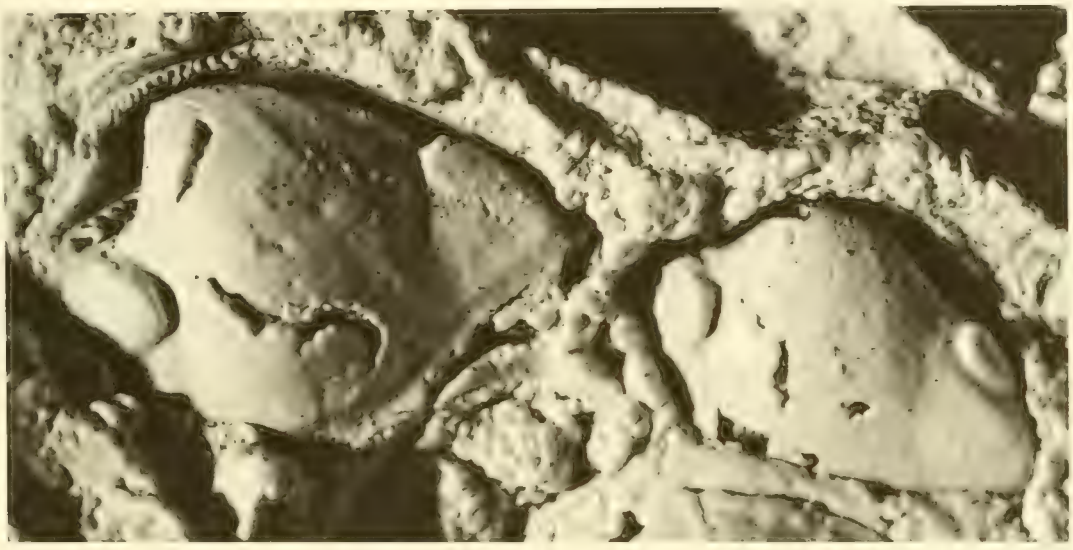

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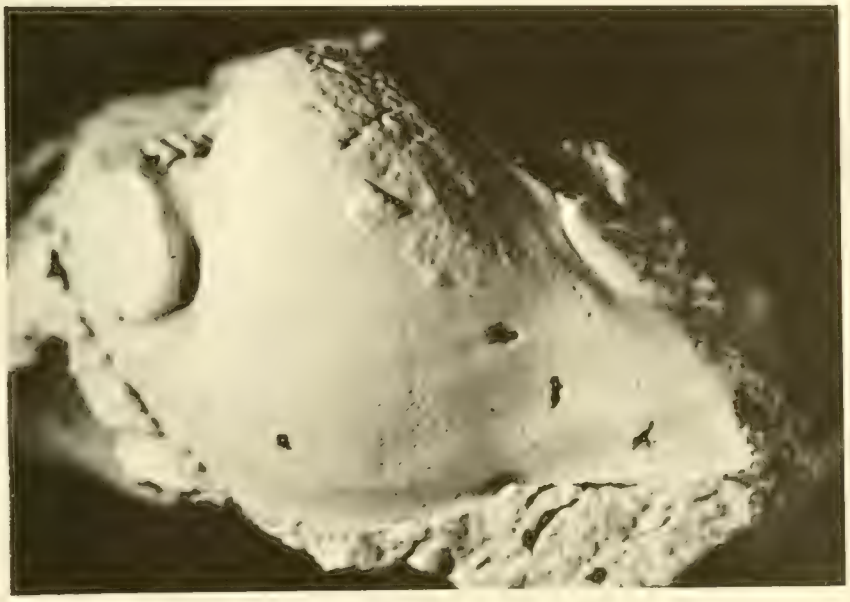

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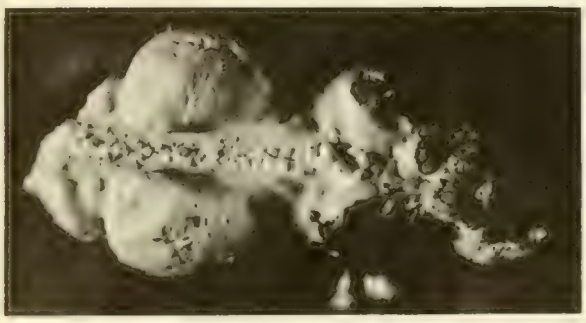

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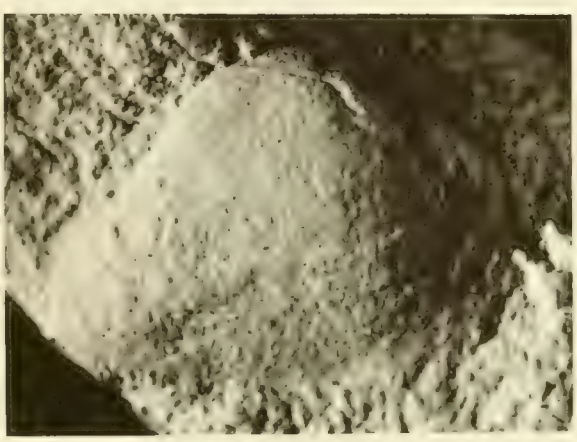

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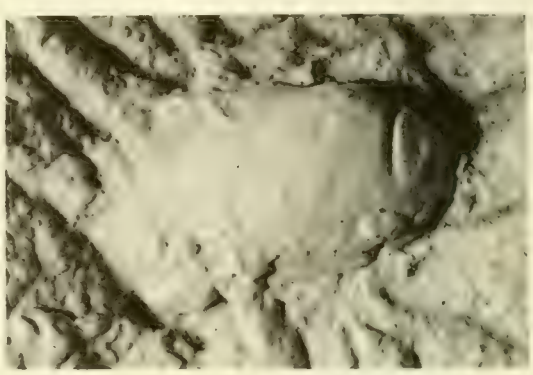

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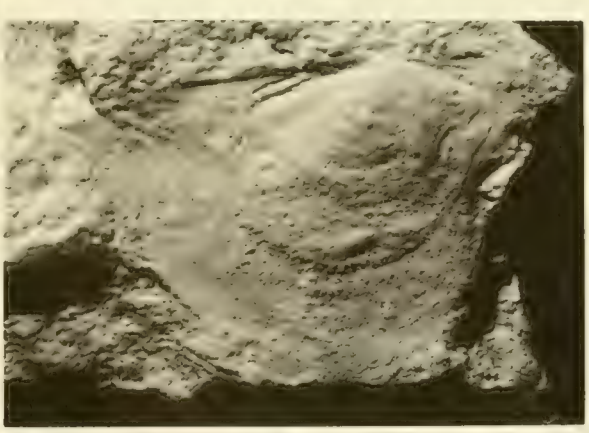

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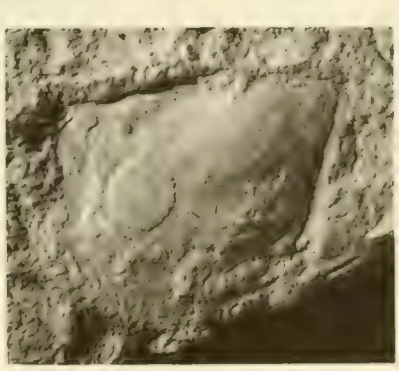

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PLATE 24

All figures are ×4 except figs. 5, 6 (×2).

Figs. 1-3. *Tancrediopsis cuneata* (Hall) ..... p. 113

1. YPM 25969, Loc. 97 (4) (A-6413).
2. YPM 25970, Loc. 84 (A-6402).
3. YPM 25971, Loc. 75 (A-6395).

Fig. 4. Genus *Nuculites* ..... p. 117

4. YPM 25972, Loc. 34-A (A-6345).

Figs. 5-7. *Pterinea* (*Caritodens*) *demissa* (Conrad) ..... p. 124

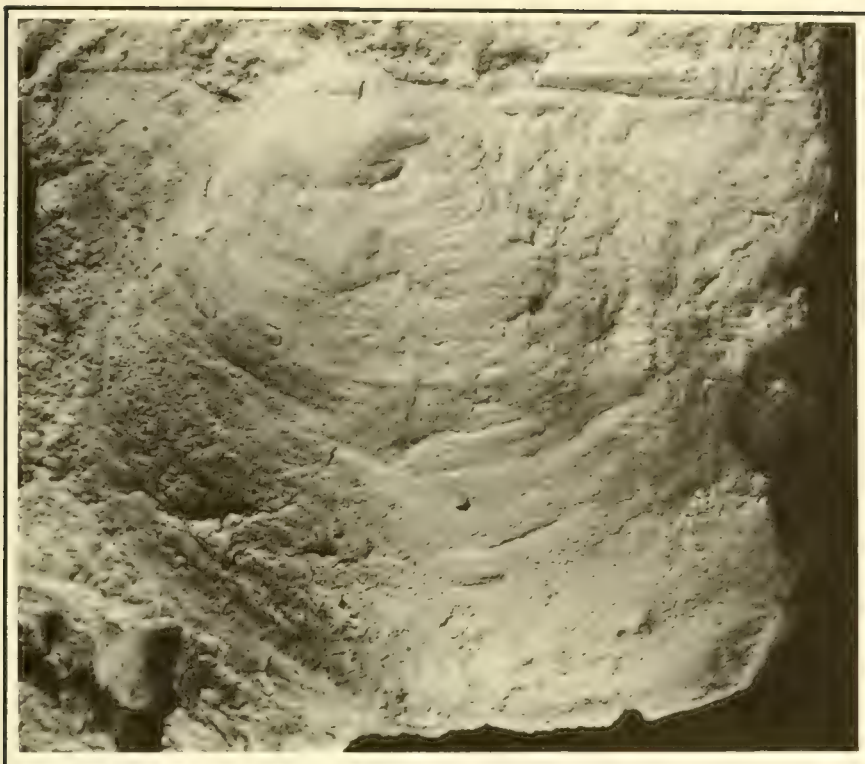
5. YPM 25973, Loc. 152 (A-6548), internal mold (natural) of right valve showing pronounced posterior lateral socket.
6. YPM 25974, Loc. 152 (A-6548), internal mold (natural) of right valve showing partial impression of large posterior adductor.
7. YPM 25975, Loc. 203 (A-6303), showing obliquely prosoclinal shape characteristic of smaller species.

PLATE 25

All figures are ×2 except fig. 3 (×4).

Figs. 1-5. *Pterinea* (*Caritodens*) *demissa* (Conrad) ..... p. 124

1. YPM 25976, Loc. 203 (A-6303), showing obtuse, rounded shape characteristic of larger specimens.
2. YPM 25977, Loc. 149 (A-6455).
3. YPM 25976, similar to fig. 1 only higher magnification showing the duplivincular ligament.
4. YPM 25978, Loc. 150 (A-6456).
5. YPM 25979, Loc. 203 (A-6303), internal mold (natural) of left valve showing impression of posterior lateral tooth or jugum.



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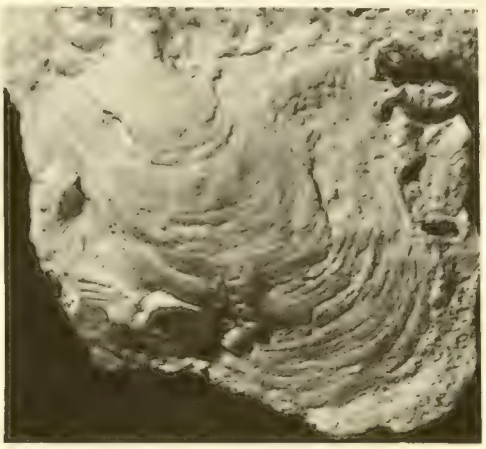

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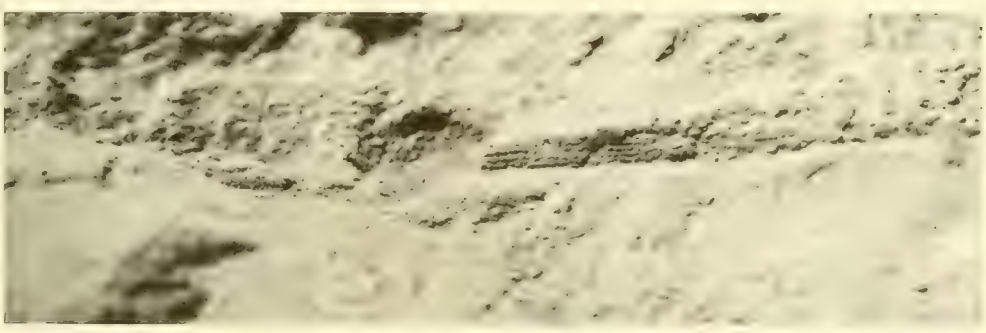

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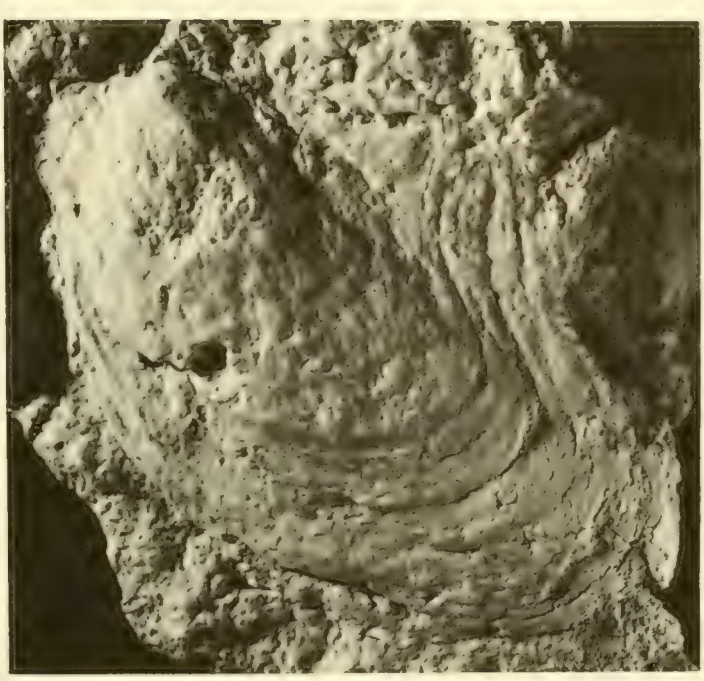

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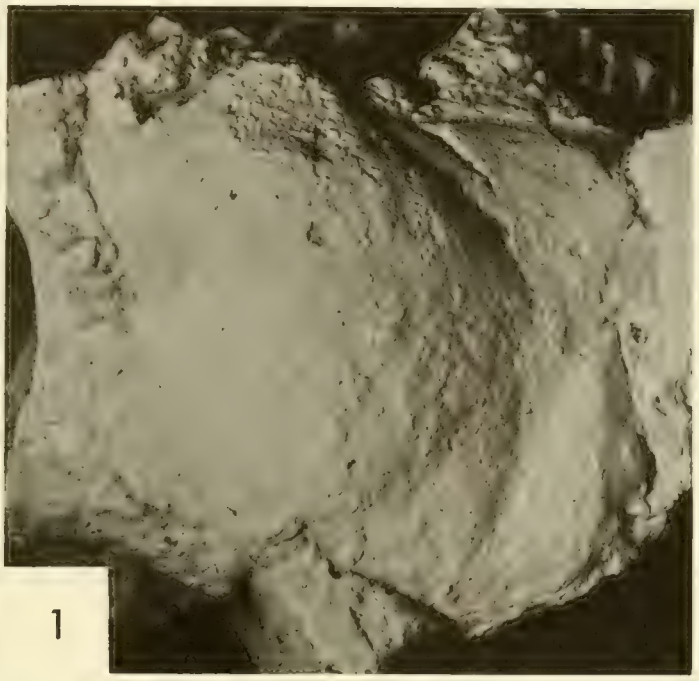

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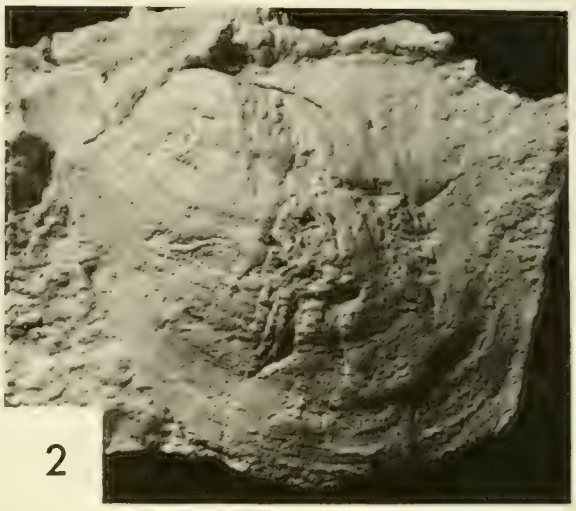

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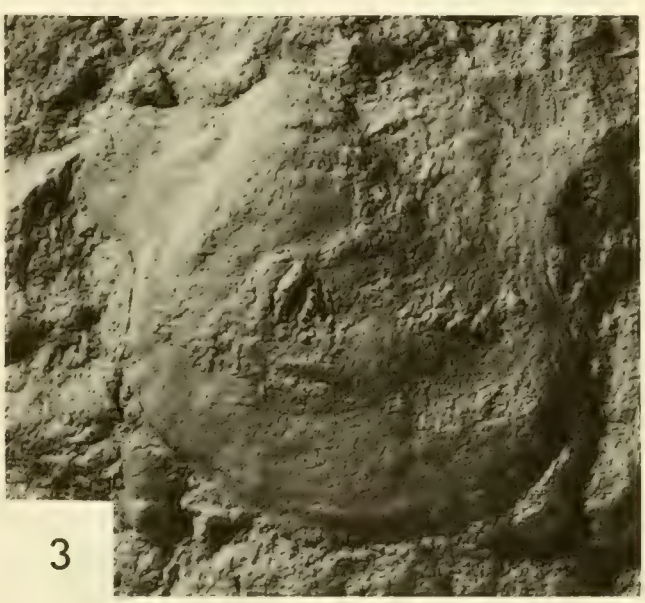

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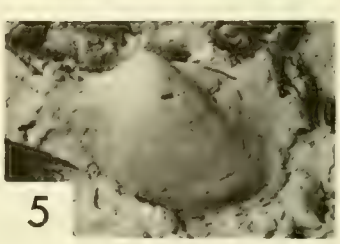

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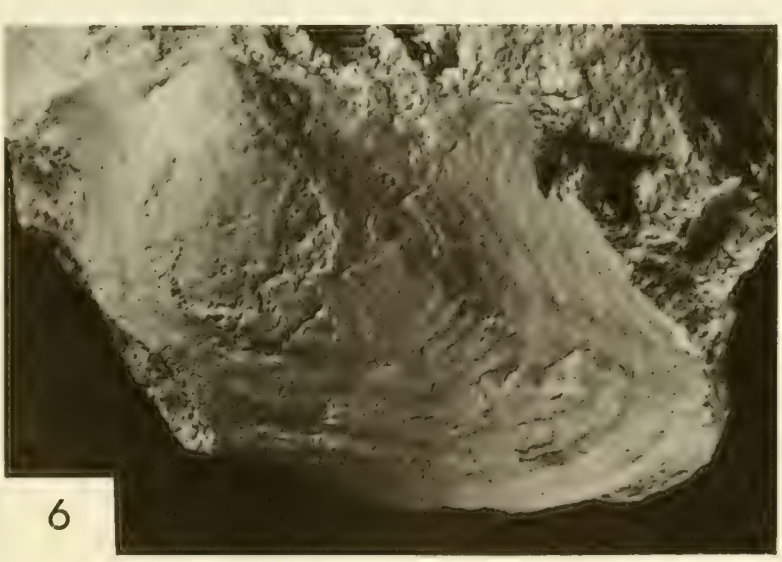

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PLATE 26

All figures are ×2.

Figs. 1-6. *Pterinea* (*Caritodens*) *demissa* (Conrad) ..... p. 124

1. YPM 25980, Loc. 185 (A-6484).
2. YPM 25981, Loc. 203 (A-6309).
3. YPM 25982, Loc. 203 (A-6304).
4. YPM 25983, Loc. 147 (A-6453).
5. YPM 25984, Loc. 186 (A-6323).
6. YPM 25985, Loc. 203 (A-6306).

Fig. 7. Probable *Pterinea* (*Caritodens*) *demissa* (Conrad) ..... p. 124

7. YPM 25986, Loc. 181 (A-6480).

PLATE 27

All figures are ×2.

Fig. 1. *Pterinea* (*Caritodens*) *demissa* (Conrad) ..... p. 124

1. YPM 25987, Loc. 170 (A-6470).

Fig. 2. Probable *Pterinea* sp. ..... p. 124

2. YPM 25988, Loc. 178 (A-6477).

Figs. 3-6. *Ischyrodonta truncata* Ulrich ..... p. 130

3. YPM 25989, Loc. 192 (A-6489).
4. YPM 25990, Loc. 203 (A-6306).
5. YPM 25991, Loc. 203 (A-6311).
6. YPM 25992, Loc. 203 (A-6302), internal mold (natural) showing impression of small, rounded pedal retractors.

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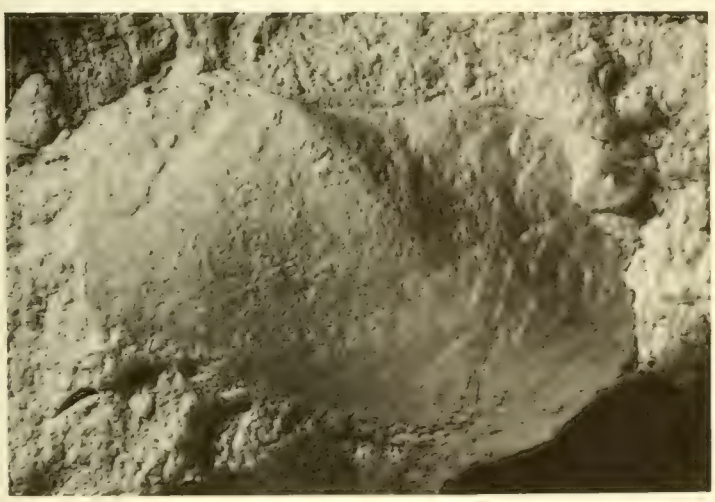

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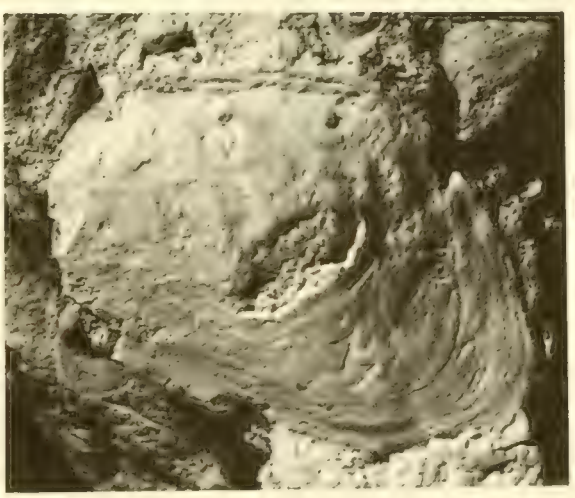

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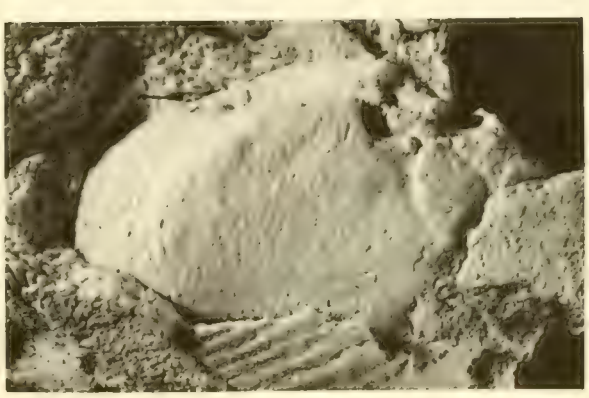

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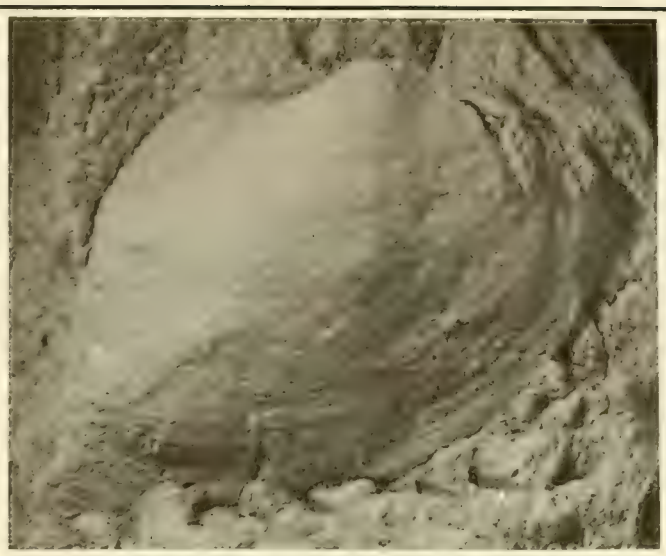

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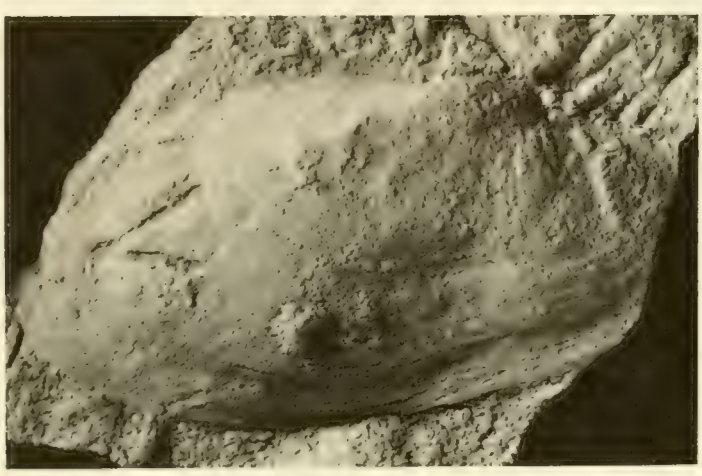

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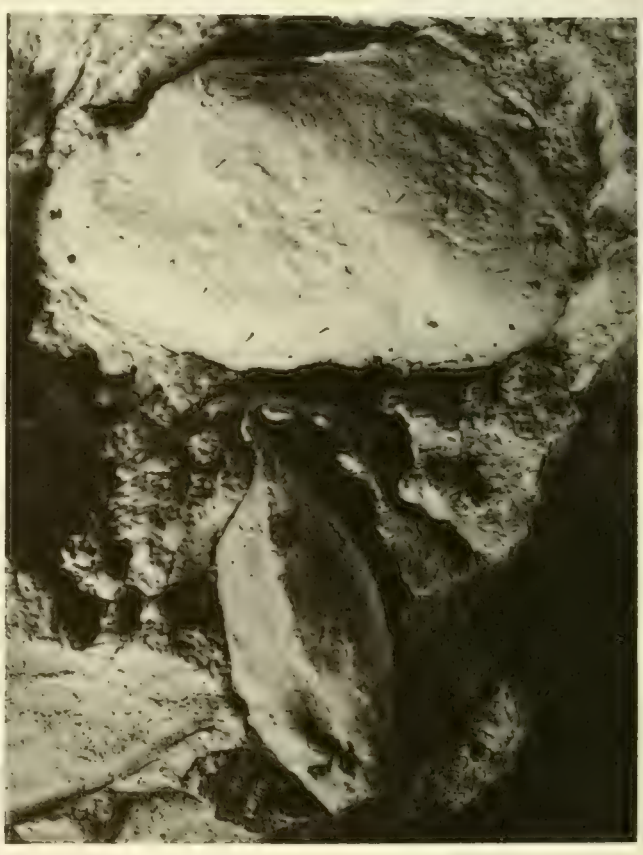

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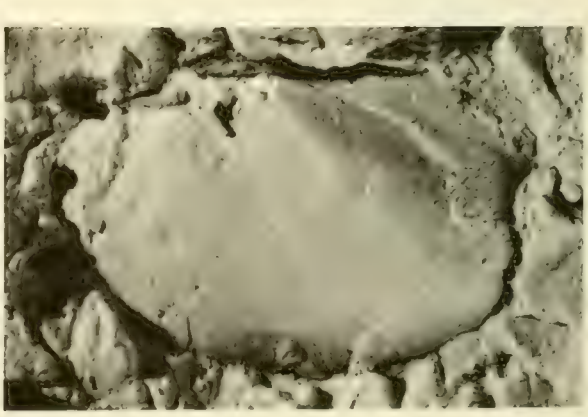

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PLATE 28

All figures are ×2 except fig. 5 (×4).

Figs. 1-6. *Ischyrodonta truncata* Ulrich ..... p. 130

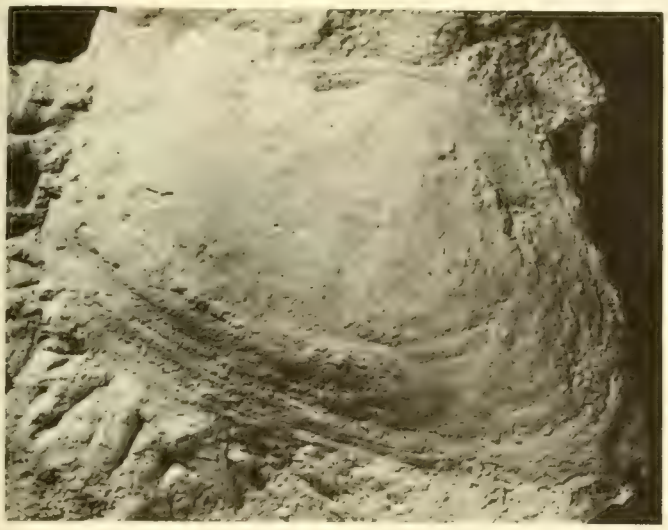
1. YPM 25993, Loc. 98 (A-6414).
2. YPM 25994, Loc. 200 (A-6496).
3. YPM 25995, Loc. 203 (A-6307), showing impression of possible worm tubes at the inhalent opening.
4. (top) — YPM 25996, Loc. 203 (A-6309).
   (bottom) — YPM 25997, Loc. 203 (A-6309).
5. YPM 25998, Loc. 87 (A-6404), internal mold (natural) of left valve showing impression of cardinal dentition.
6. YPM 25998 — Similar to fig. 5, except lower magnification.

PLATE 29

All figures are ×2.

Figs. 1-6. *Ischyrodonta truncata* Ulrich ..... p. 130

1. YPM 25999, Loc. 152 (A-6458).
2. YPM 26000, Loc. 38 (A-6364).
3. YPM 26001, Loc. 182 (A-6481), latex impression showing possible worm tubes at the inhalent opening.
4. YPM 26002, Loc. 203 (A-6309).
5. YPM 26003, Loc. 99 (A-6415).
6. YPM 26004, Loc. 203 (A-6310).



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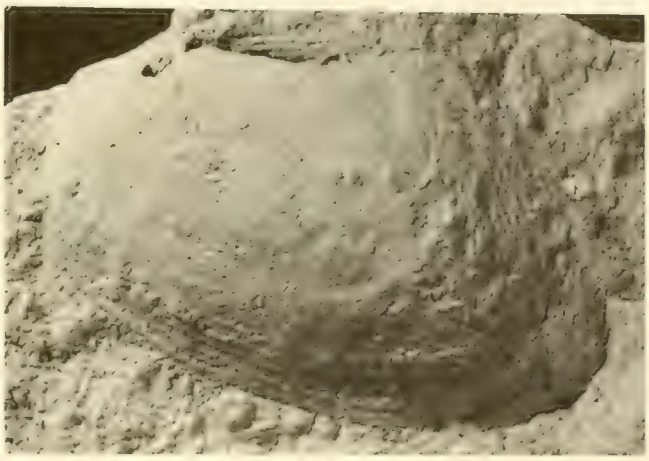

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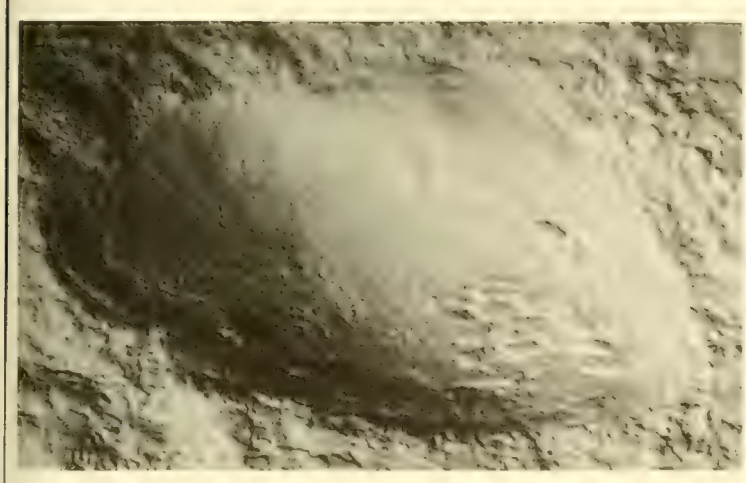

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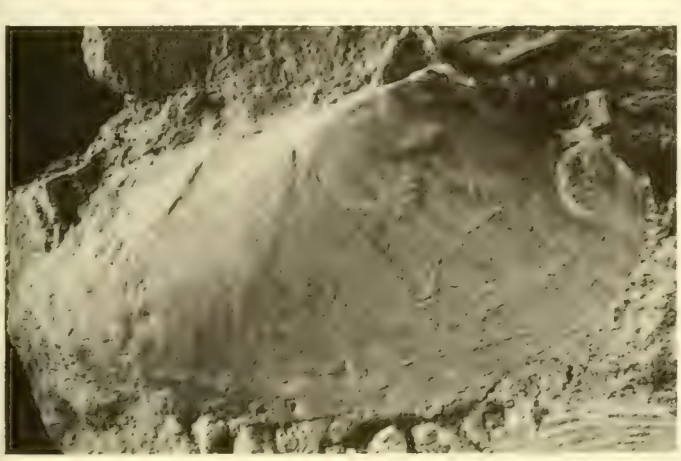

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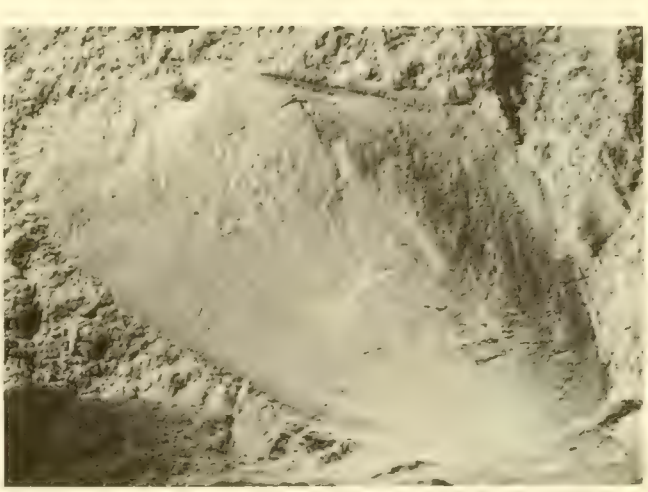

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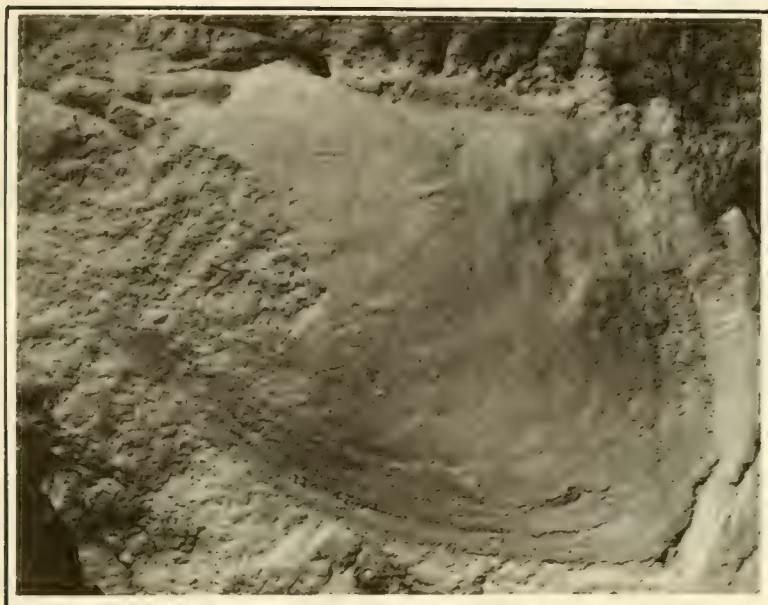

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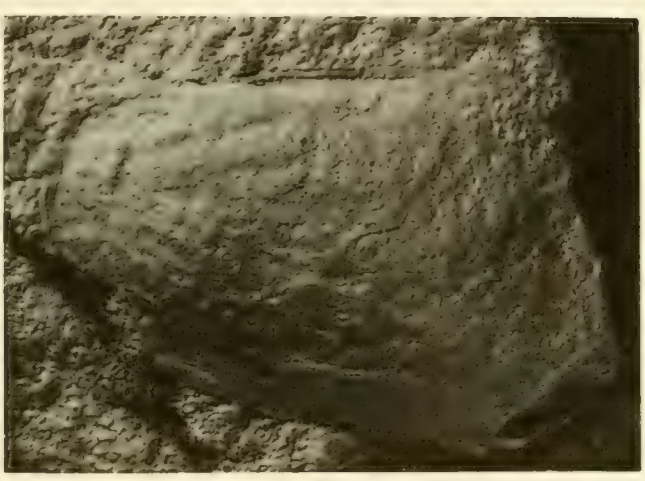

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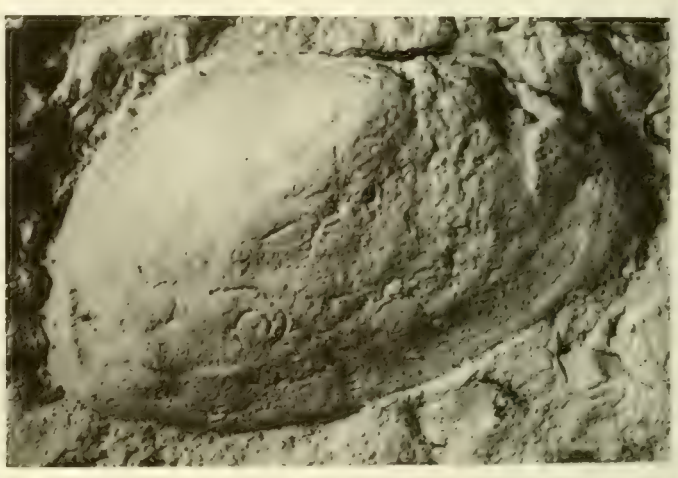

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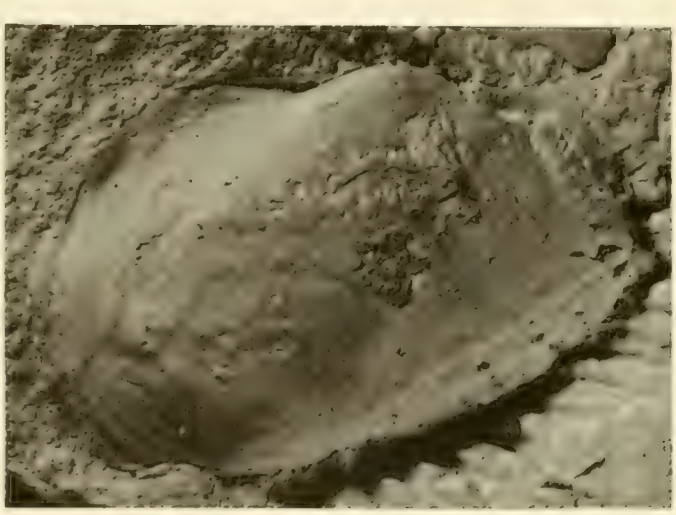

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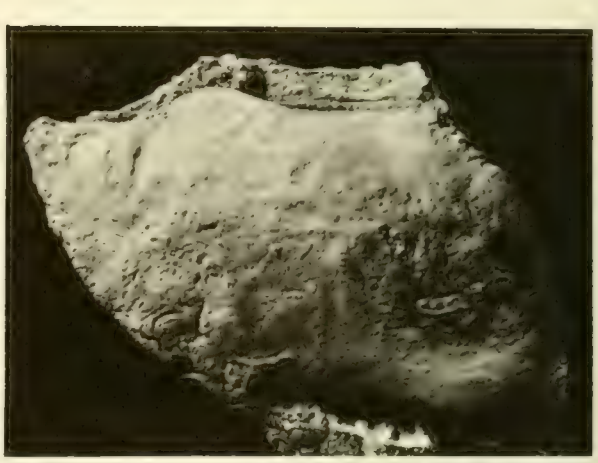

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PLATE 30

All figures are ×2.

Figs. 1-6. *Ischyrodonta truncata* Ulrich ..... p. 130

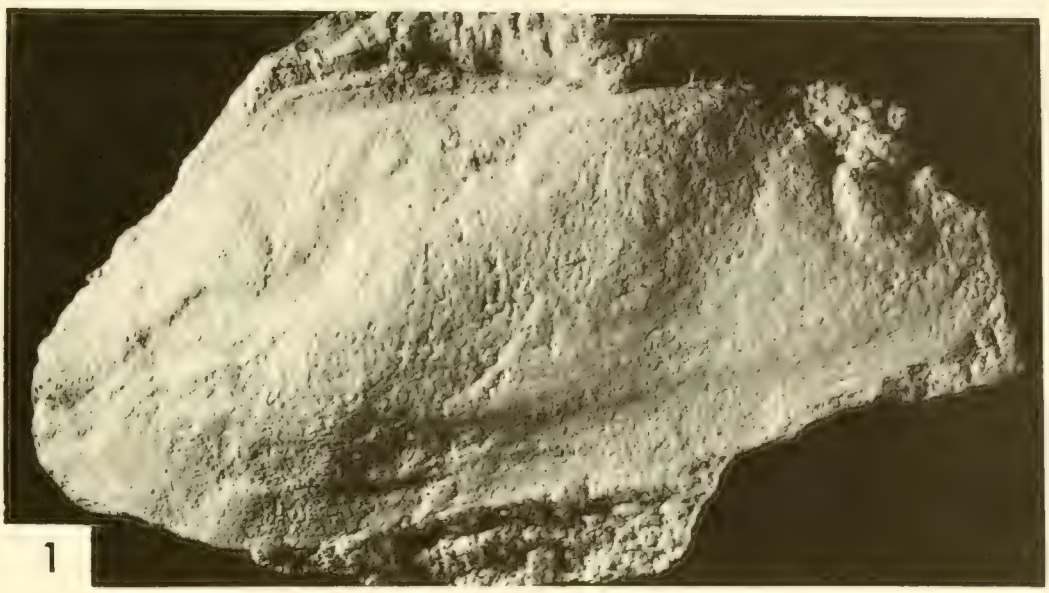
1. YPM 26005, Loc. 152 (A-6458).
2. YPM 26006, Loc. 140 (A-6447), latex impression.
3. YPM 26007, Loc. 203 (A-6308).
4. YPM 26008, Loc. 203 (A-6309).
5. YPM 26009, Loc. 98 (A-6414).
6. YPM 26010, Loc. 203 (A-6303), showing amphidetic, dupli-vincular ligament.

PLATE 31

All figures are ×2 except fig. 3 (×1.5).

Figs. 1-3. *Modiolopsis modiolaris* (Conrad) ..... p. 127

1. YPM 26011, Loc. 203 (A-6303), showing impression of an irregular "U"-shaped tube at the approximate position of the inhalent current.
2. YPM 26012, Loc. 203 (A-6303).
3. YPM 26013, Loc. 203 (A-6307).



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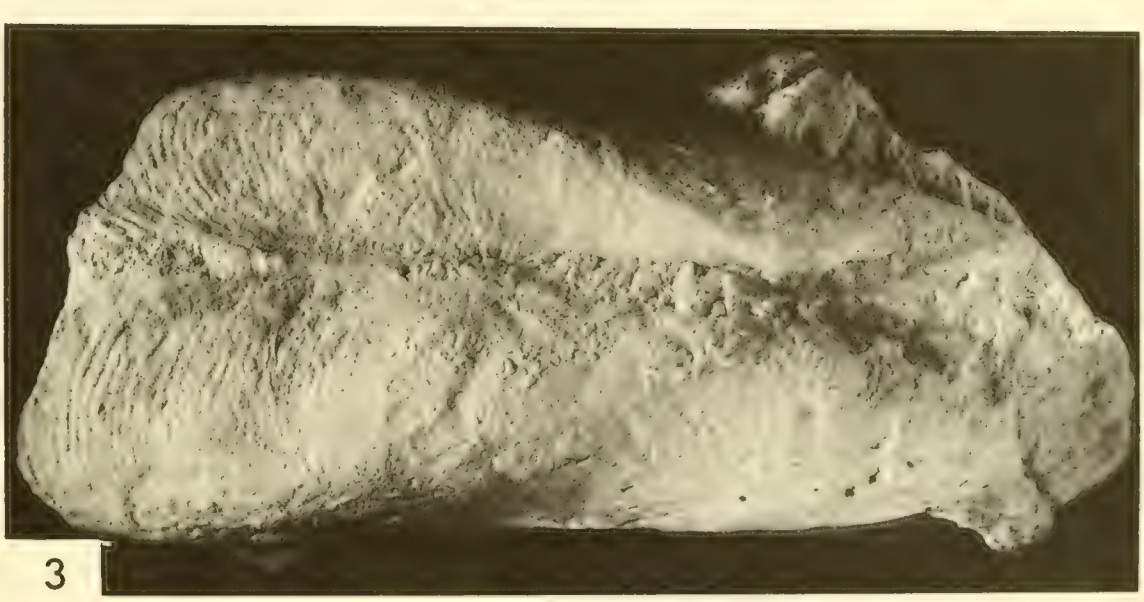

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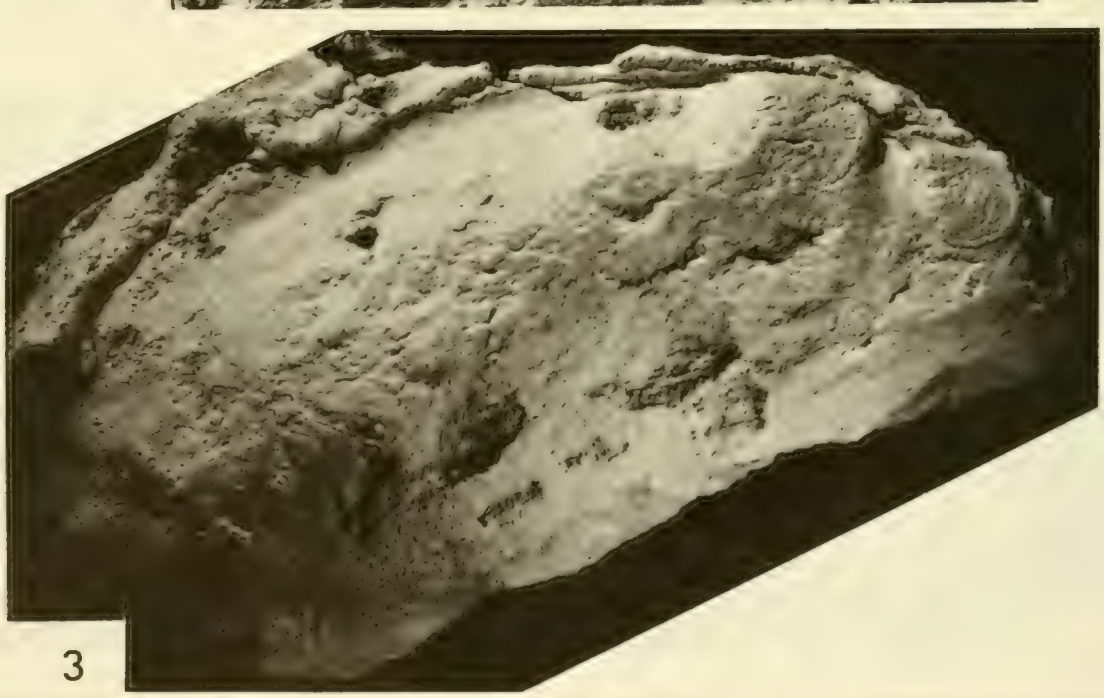

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PLATE 32

All figures are ×2.

Figs. 1, 3. *Modiolopsis modiolaris* (Conrad) ..... p. 127

1. YPM 26014, Loc. 63 (B) (A-6383).
3. YPM 26016, Loc. 203 (A-6305), internal mold (natural) showing impression of elongate, broad opisthodetic ligament.

Fig. 2. Probable *Modiolopsis modiolaris* (Conrad) ..... p. 127

2. YPM 26015, Loc. 52 (A-6380), possibly another species (cf. *M. sinuata*).

PLATE 33

All figures are ×2 except fig. 2 (×1.5).

Figs. 1-3. *Modiolopsis modiolaris* (Conrad) ..... p. 127

1. YPM 26017, Loc. 203 (A-6303).
2. YPM 26018, Loc. 171 (A-6471).
3. YPM 26019, Loc. 203 (A-6303).

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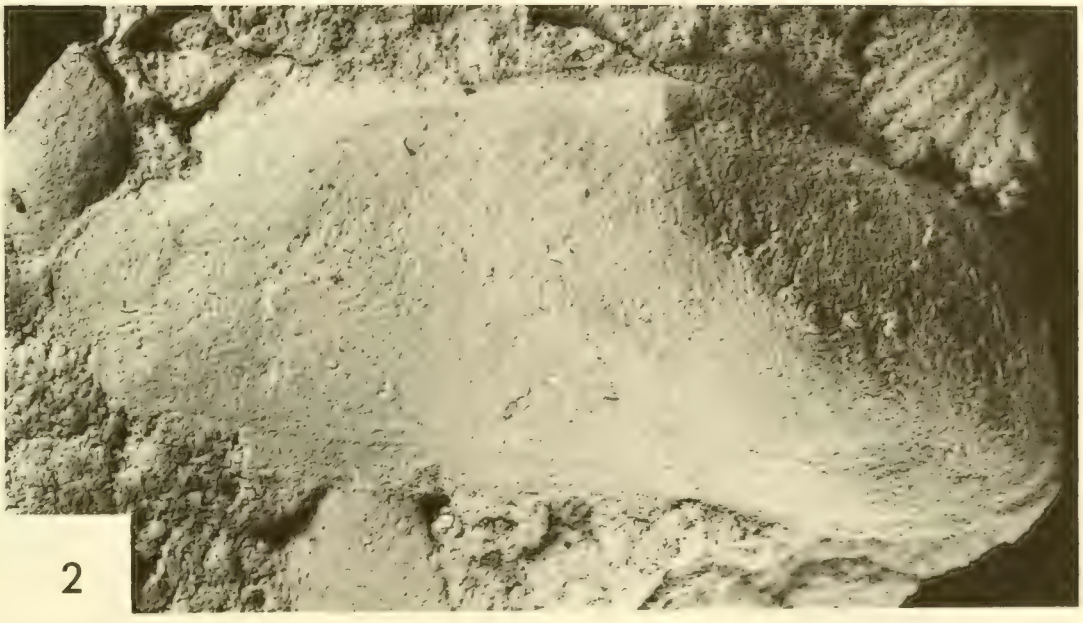

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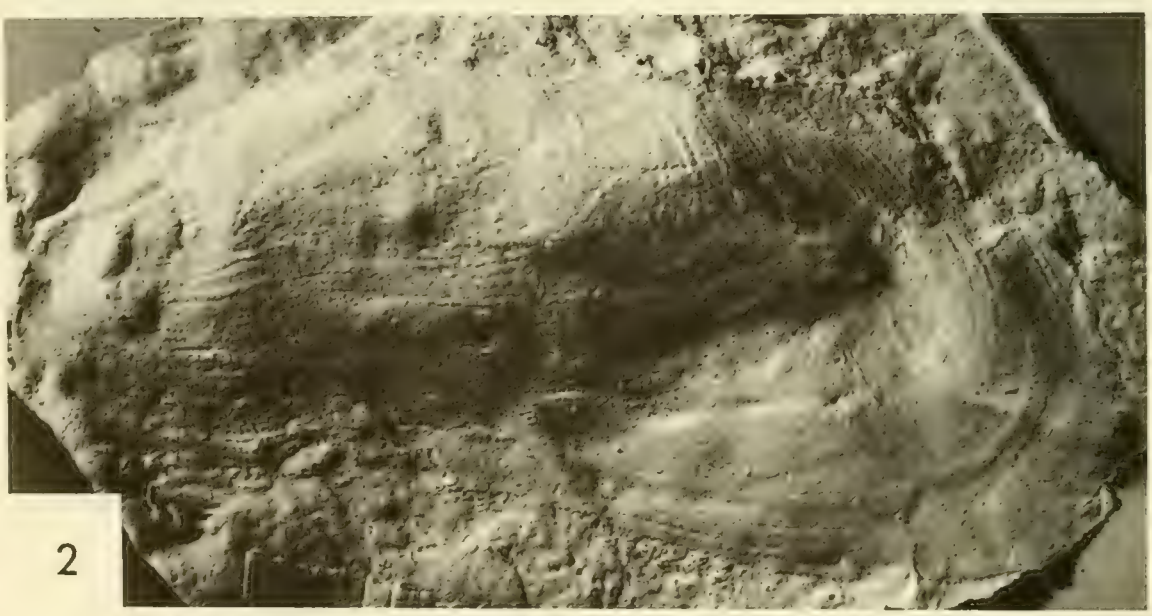

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PLATE 34

All figures are ×2.

Figs. 1-3. *Modiolopsis modiolaris* (Conrad) ..... p. 127

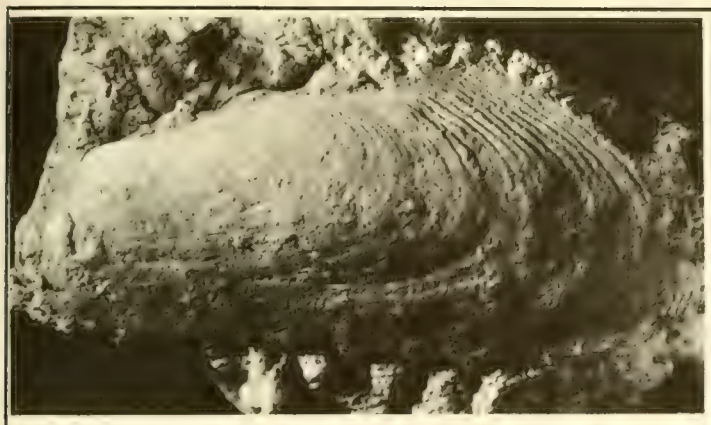
1. YPM 26020, Loc. 149 (A-6455).
2. YPM 26021, Loc. 203 (A-6301), latex impression.
3. YPM 26022, Loc. 186 (A-6323).

PLATE 35

All figures are ×2.

Figs. 1-4. *Modiolopsis modiolaris* (Conrad) ..... p. 127

1. YPM 26023, Loc. 147 (A-6453).
2. YPM 26024, Loc. 125 (A-6433), possibly another species (cf. *M. concentrica*).
3. YPM 26025, Loc. 87 (A-6404).
4. YPM 26026, Loc. 203 (A-6302), showing shape variation resulting from tectonic distortion.



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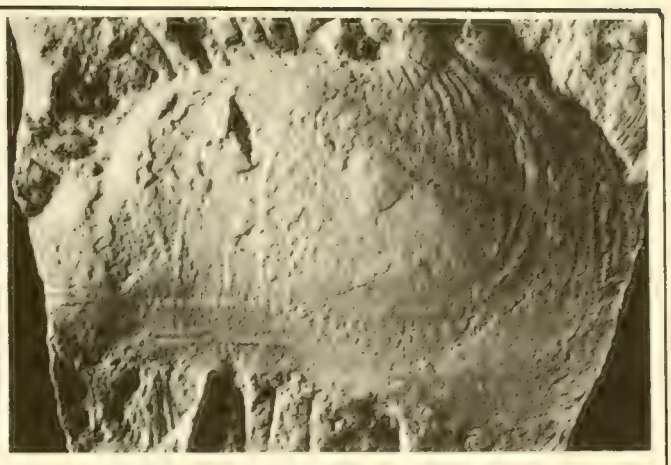

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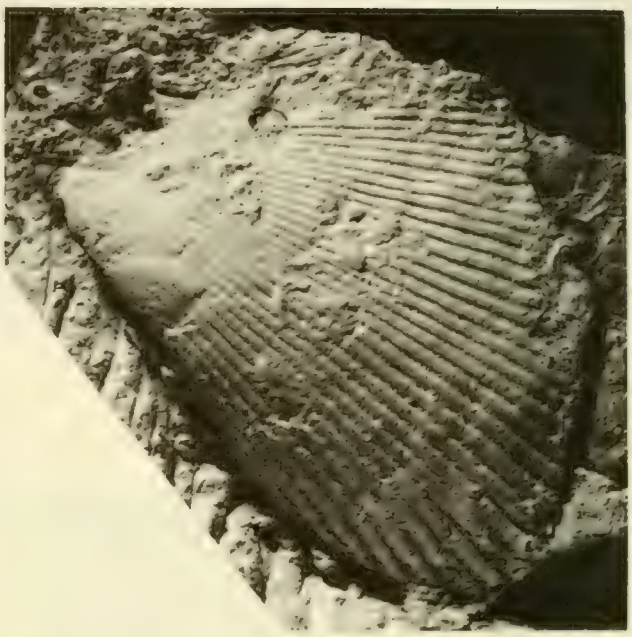

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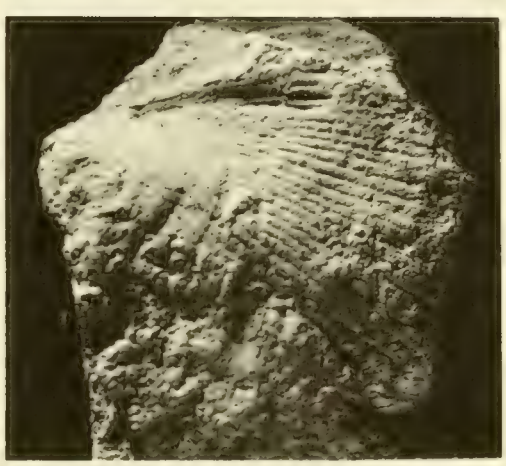

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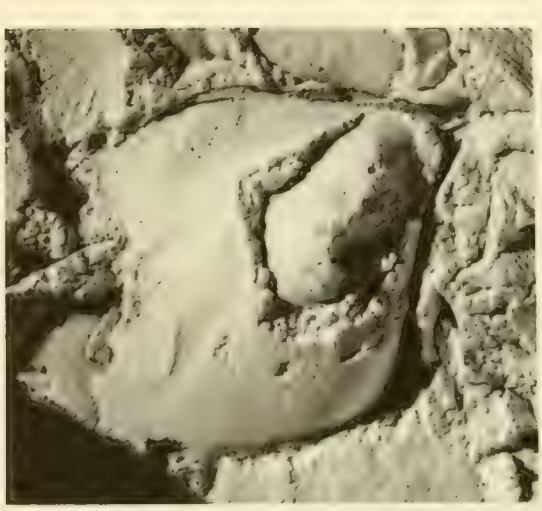

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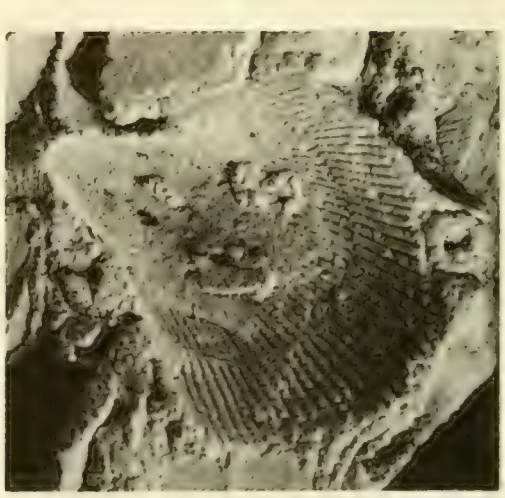

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PLATE 36

All figures are ×2.

Figs. 1-6. *Ambonychia radiata* Hall ..... p. 117

1. YPM 26027, Loc. 62 (H) (A-6382), showing striated ligament.
2. YPM 26028, Loc. 77-A (A-6397).
3. YPM 26029, Loc. 82 (A-6400), showing posterior lateral teeth.
4. YPM 26030, Loc. 37 (A-6359).
5. YPM 26031, Loc. 75 (A-6395), internal mold (natural) showing impression of cardinal and lateral teeth and part of posterior adductor muscle scar.
6. YPM 26031, external mold (natural) of fig. 5. Lighting from bottom.

PLATE 37

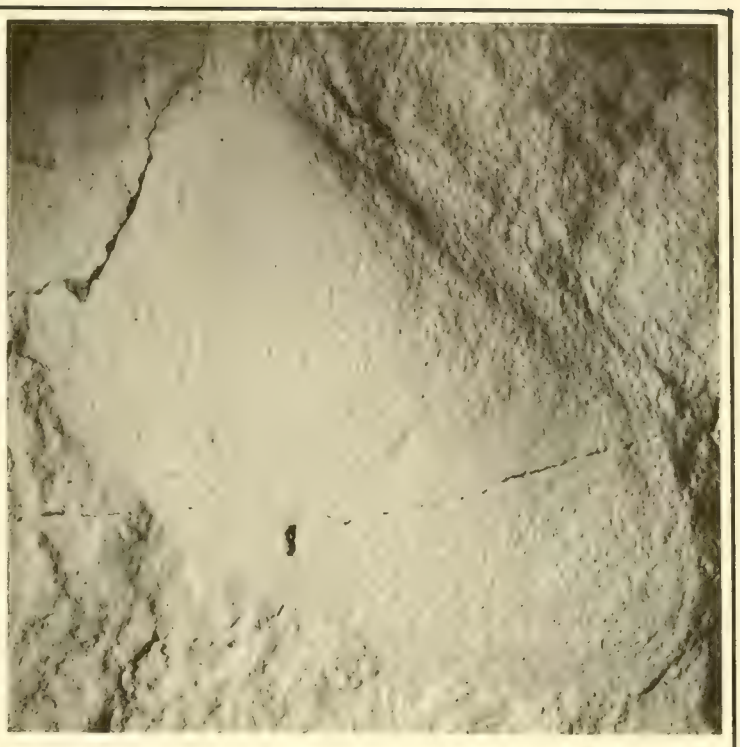
All figures are ×2 except figs. 2, 3 (×1).

Figs. 1-3. *Cyrtodonta*? ..... p. 129

1. YPM 26032, Loc. 167 (A-6467).
2. YPM 26033, Loc. 167 (A-6467).
3. YPM 26034, Loc. 167 (A-6467).

Figs. 4-5. *Ambonychia praecursa* (Ulrich) ..... p. 118

4. YPM 26035, Loc. 203 (A-6302).
5. YPM 26036, Loc. 203 (A-6303).



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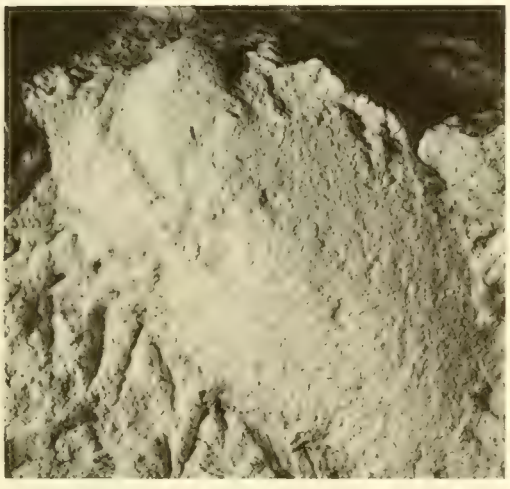

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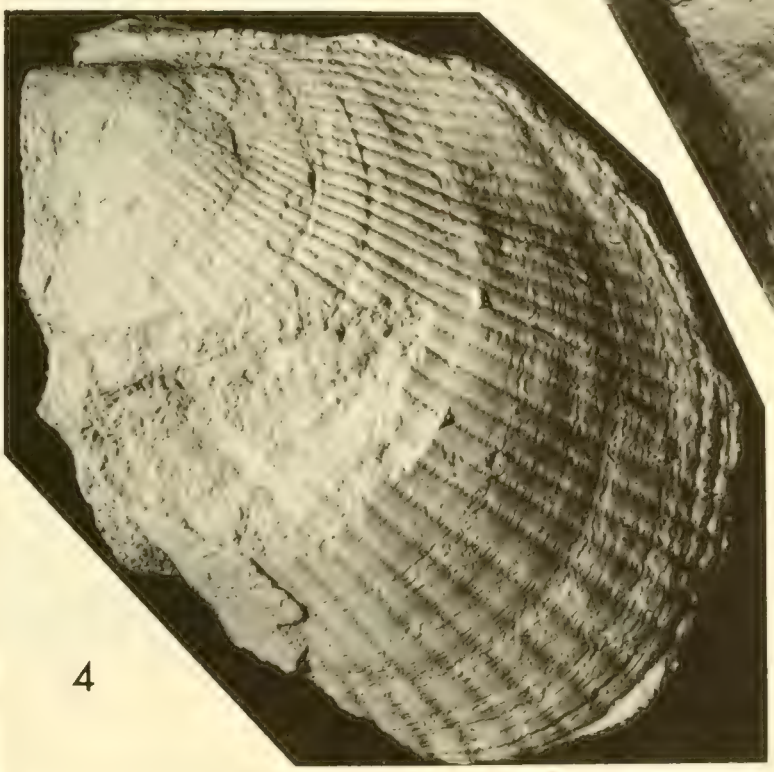

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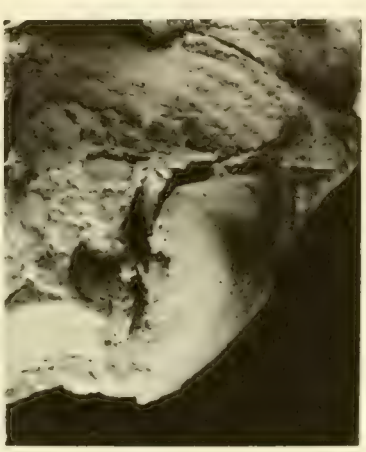

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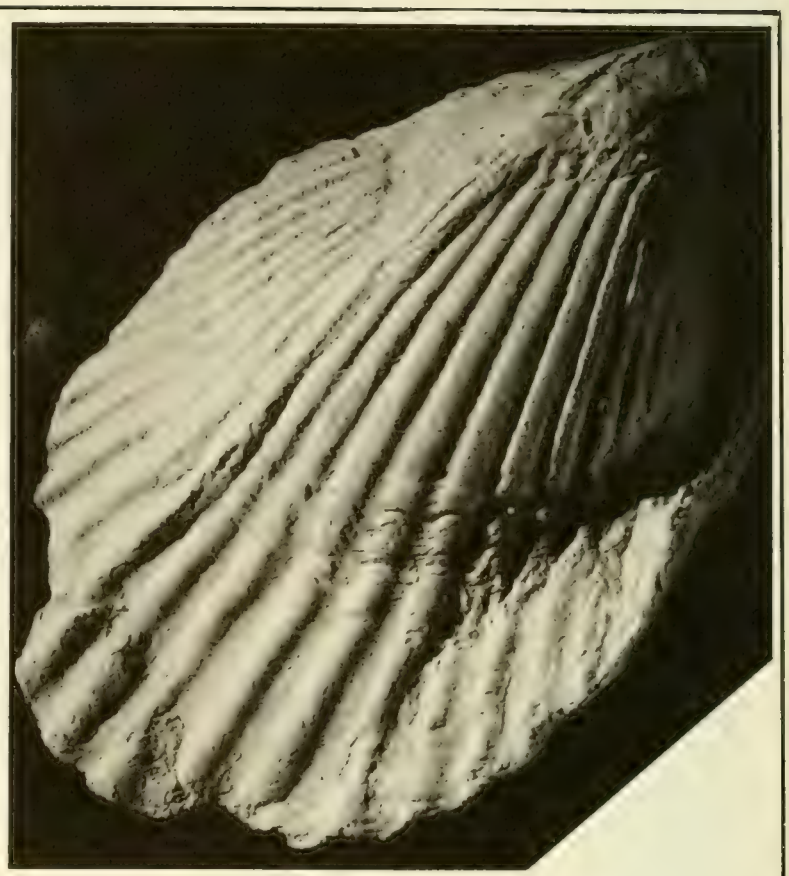

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PLATE 38

All figures are ×2 except fig. 1 (×4).

Figs. 1-2, 4-5. *Ambonychia praecursa* (Ulrich) ..... p. 118

1. YPM 26037, Loc. 87 (A-6404), internal mold (natural) showing impression of cardinal dentition.
2. YPM 26037, same as fig. 1 only lower magnification.
4. YPM 26039, Loc. 177 (A-6476).
5. YPM 26040, Loc. 75 (A-6395), showing impression of lateral teeth confined to posterior end of hinge line.

Fig. 3. ?*Ambonychia byrnesi* (Ulrich) ..... p. 123

3. YPM 26038, Loc. 75 (A-6395).

PLATE 39

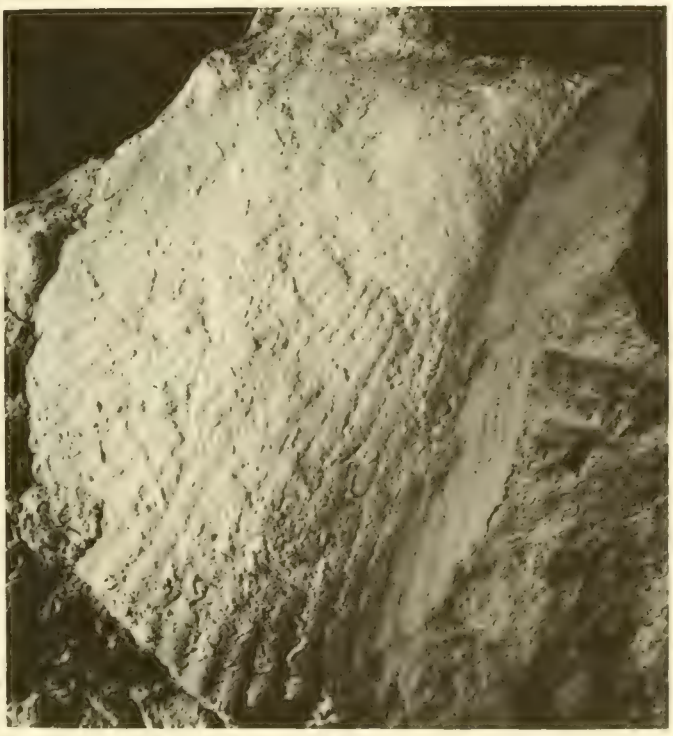
All figures are ×2.

Figs. 1-4. *Ambonychia praecursa* (Ulrich) ..... p. 118

1. YPM 26041, Loc. 93 (A-6409), showing impression of posterior lateral teeth.
2. YPM 26042, Loc. 203 (A-6306), prominent byssal gap.
3. YPM 26043, Loc. 203 (A-6303).
4. YPM 26044, Loc. 203 (A-6303).

1

2



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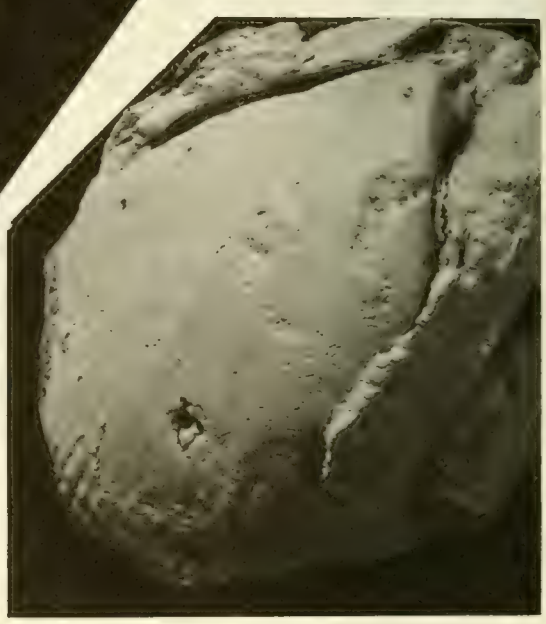

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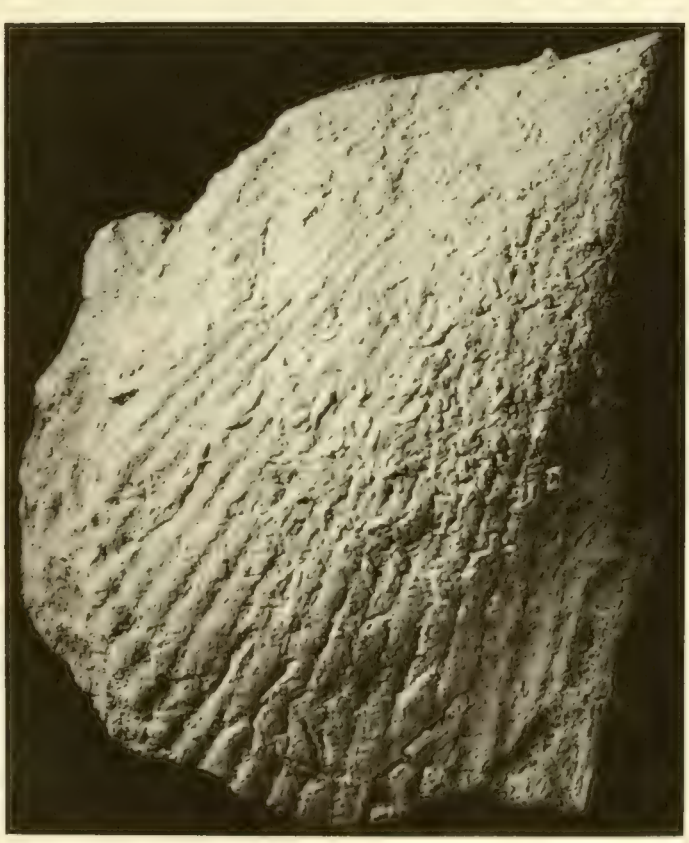

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PLATE 40

All figures are ×2.

Figs. 1-4. *Ambonychia praecursa* (Ulrich) ..... p. 118

1. YPM 26045, Loc. 75 (A-6395).
2. YPM 26046, Loc. 203 (A-6303).
3. YPM 26047, Loc. 203 (A-886).
4. YPM 26048, Loc. 203 (A-6301).

PLATE 41

All figures are ×2.

Figs. 1-3. *Ambonychia praecursa* (Ulrich) ..... p. 118

1. YPM 26049, Loc. 203 (A-6302).
2. YPM 26050, Loc. 75 (A-6395), bifurcation of some ribs near the hinge line.
3. YPM 26051, Loc. 75 (A-6395).

1

2

3

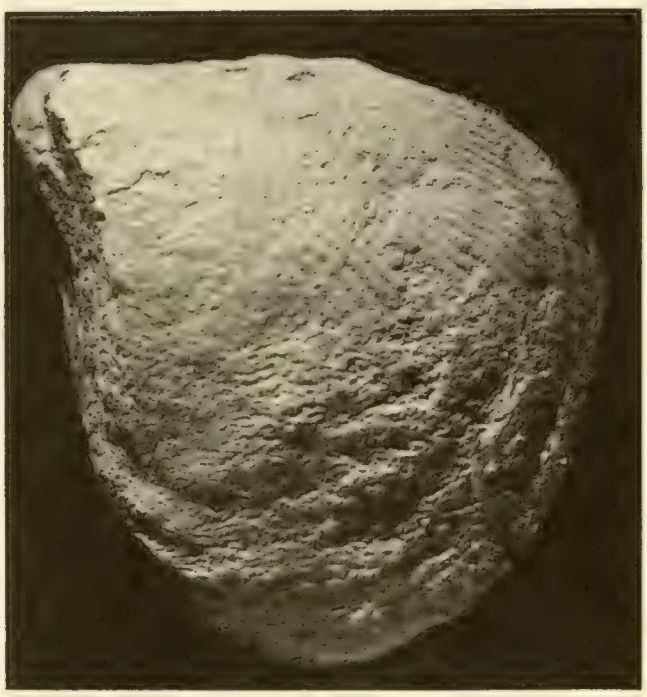

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PLATE 42

All figures are ×2.

Figs. 1-2. *Ambonychia cultrata* (Ulrich) ..... p. 122

1. YPM 26052, Loc. 145 (A-6452).
2. YPM 26053, Loc. 152 (A-6458), showing impression of longitudinally striated ligament.

Figs. 3-4. *Ambonychia praecursa* (Ulrich) ..... p. 118

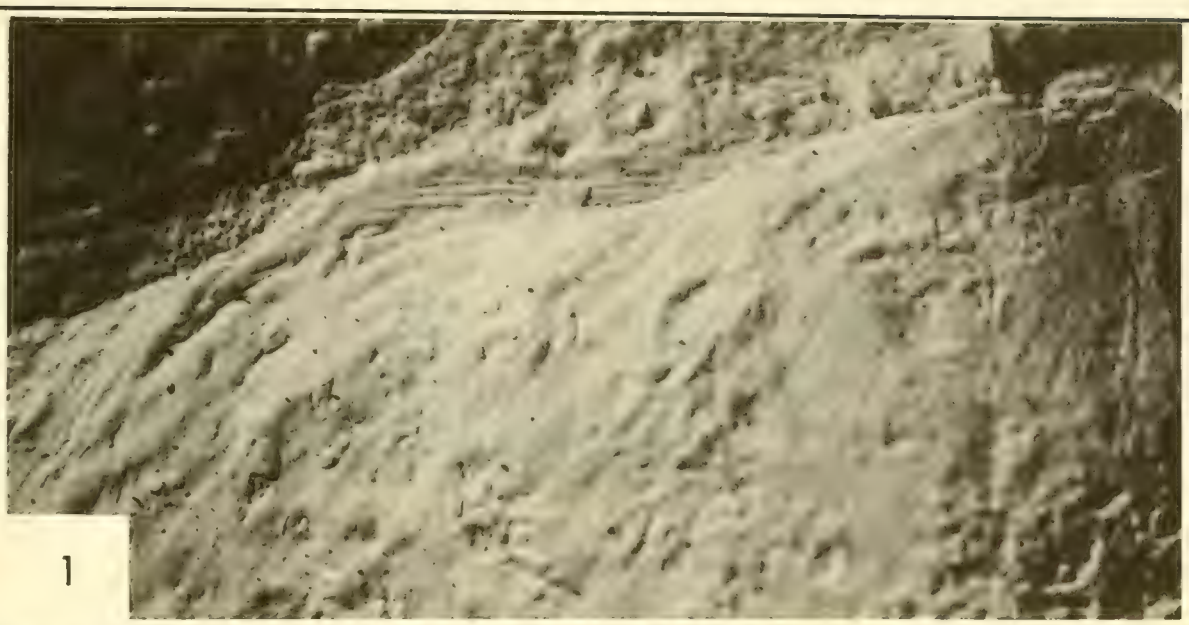
3. YPM 26054, Loc. 203 (A-6308).
4. YPM 26055, Loc. 203 (A-6303).

PLATE 43

All figures are ×2 except fig. 1 (×4), fig. 4 (×1).

Figs. 1-4. *Ambonychia cultrata* (Ulrich) ..... p. 122

1. YPM 26056, Loc. 141 (A-6448), impression of longitudinally striated ligament.
2. YPM 26056, same as fig. 1 only lower magnification.
3. YPM 26057, Loc. 141 (A-6448), impression of striated ligament.
4. YPM 26058, Loc. 141 (A-6448).



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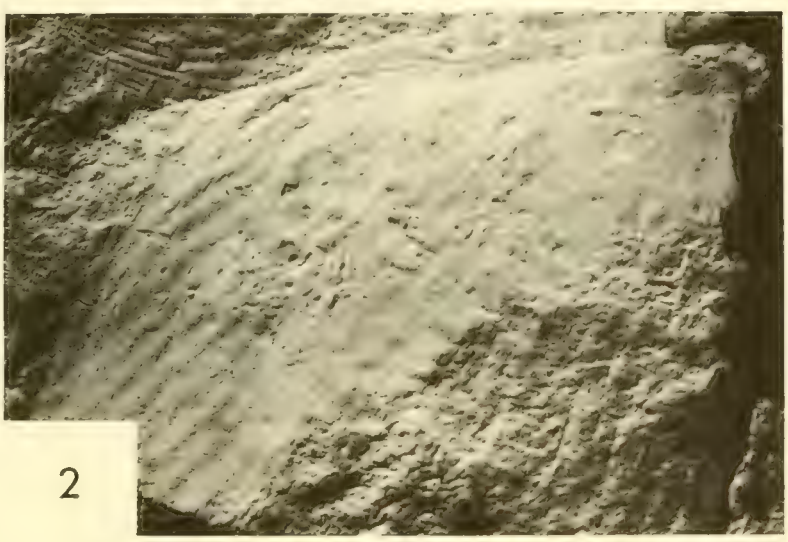

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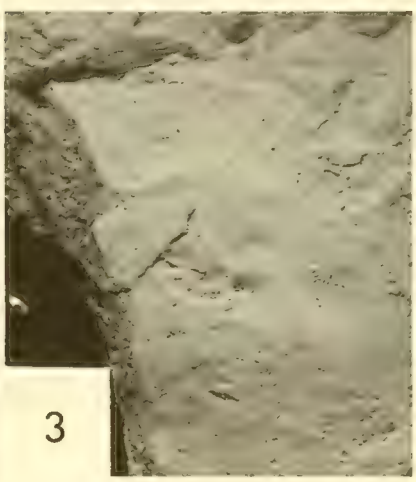

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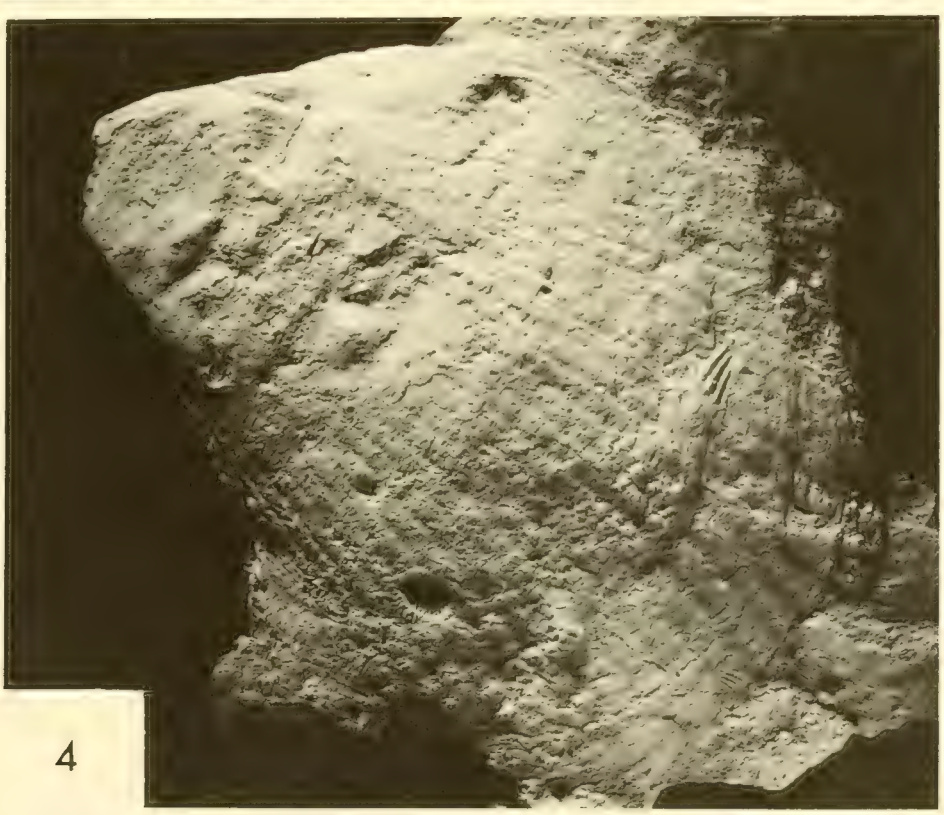

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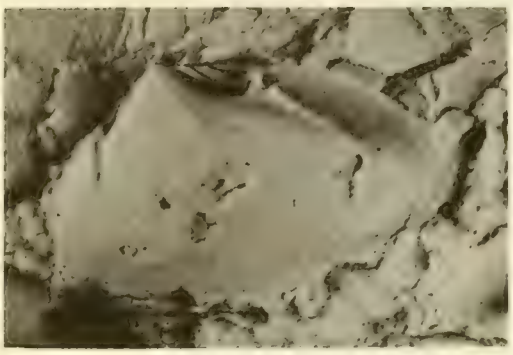

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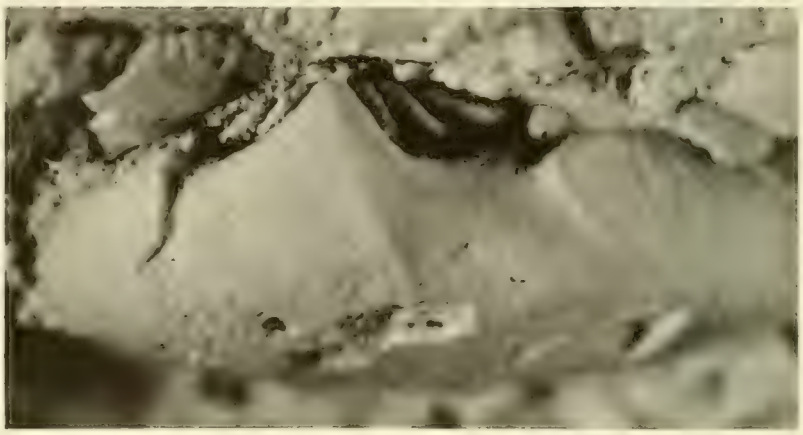

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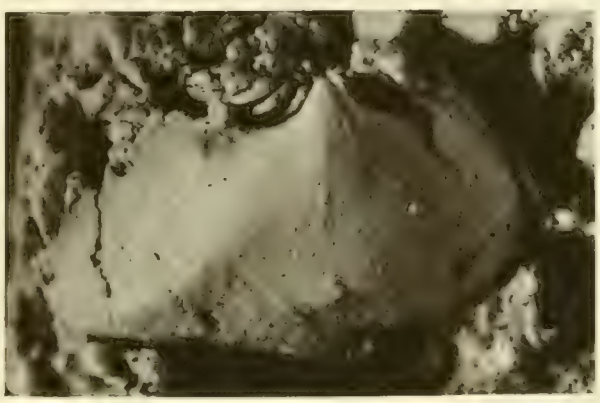

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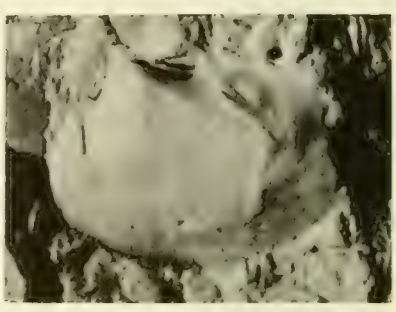

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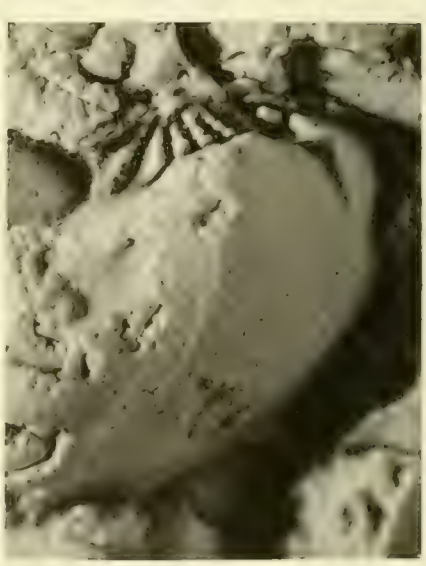

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PLATE 44

All figures are ×4 except figs. 1, 5 (×2).

Figs. 1-7. *Lyrodesma poststriatum* (Emmons) ..... p. 132

1. YPM 26059, Loc. 37 (A-6359).
2. YPM 26059, same specimen as fig. 1 only higher magnification showing impression of adductor and pedal muscle scars and prominent schizodont teeth.
3. YPM 26060, Loc. 97 (11) (A-6413).
4. YPM 26061, Loc. 77-A (A-6397), showing impression of well-marked longitudinal striae on each tooth.
5. YPM 26062, Loc. 37 (A-6359), showing impression of pallial line with distinct impression of a small, posteroventral pallial sinus.
6. YPM 26063, Loc. 149 (A-6455), showing impression of coarse radial ribs at posterodorsal edge of shell.
7. YPM 26064, Loc. 37 (A-6359).

UPPER ORDOVICIAN LOCALITIES — CENTRAL APPALACHIANS

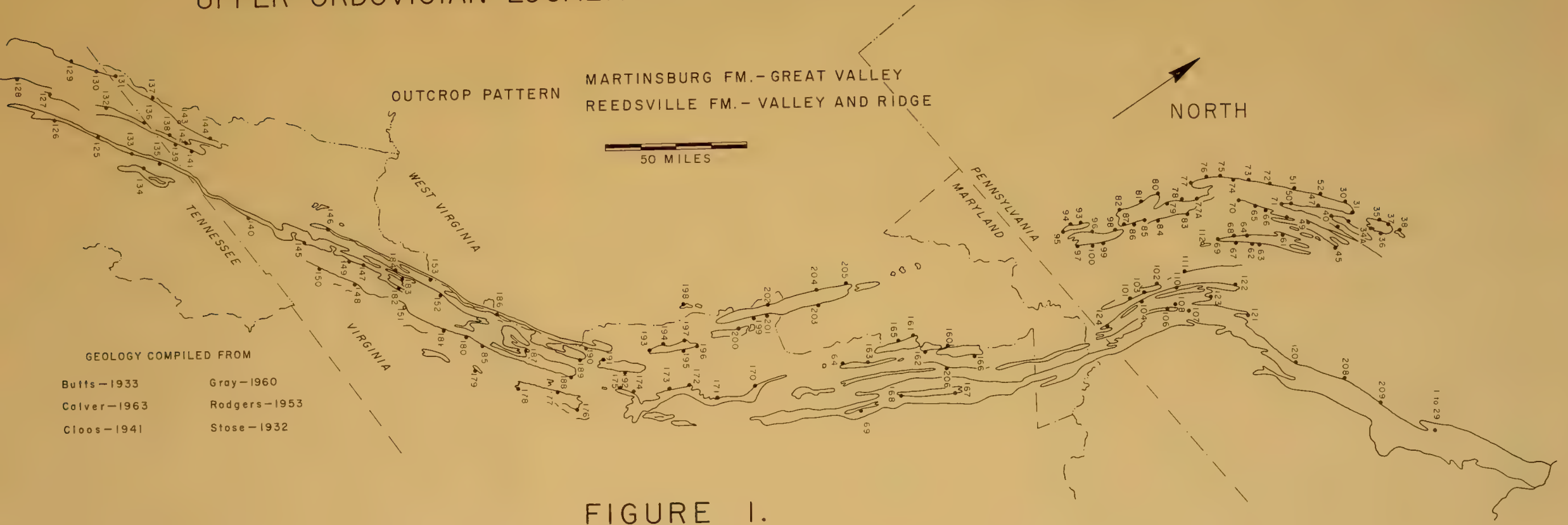

FIGURE 1.

NORTH

SOUTH

| LOCALITY | 1 | 2 | 3 | 4 | 9 | 11 | 12 | 15 | 16 | 17 | 18 | 19 | 22 | 23 | 24 | 25 | 26 | 27 | 208 | 120 | 121 | 89 | 107 | 122 | 123 | 109 | 108 | 106 | 105 | 104 | 124 | 111 | 110 | 103 | 101 | 38 | 37 | 36 | 35 | 34+34A | 32 | 33 | 42 | 30 | 31 | 39+39A | 43 | 44 | 52 | 47 | 45 | 48 | 49 | 207 | 50 | 60 | 72 | 71 | 66 | 63 | 62 | 64 | 68 | 70 | 73 | 75 | 77+77A | 112 | 78 | 83 | 79 | 84 | 86 | 81 | 82 | 87 | 98 | 92 | 90 | 99 | 100 | 97 | 93 | 94 | 95 | 186 | 160 | 204 | 162 | 161 | 163 | 164 | 167 | 168 | 169 | 205 | 204 | 203 | 202 | 201 | 199 | 200 | 170 | 171 | 172 | 173 | 174 | 175 | 198 | 196 | 195 | 197 | 194 | 193 | 192 | 191 | 190 | 189 | 188 | 177 | 187 | 178 | 186 | 180 | 179 | 181 | 152 | 153 | 184 | 183 | 151 | 147 | 148 | 149 | 150 | 145 | 140 | 144 | 143 | 142 | 141 | 137 | 138 | 139 | 131 | 130 | 135 | 132 | 125 | 133 | 130 | 129 | 127 | 126 | 128 |
|---|---|---

UPPER ORDOVICIAN STRATIGRAPHY OF THE CENTRAL APPALACHIANS

PALINSPASTIC BASE
(AFTER DENNISON, 1961)

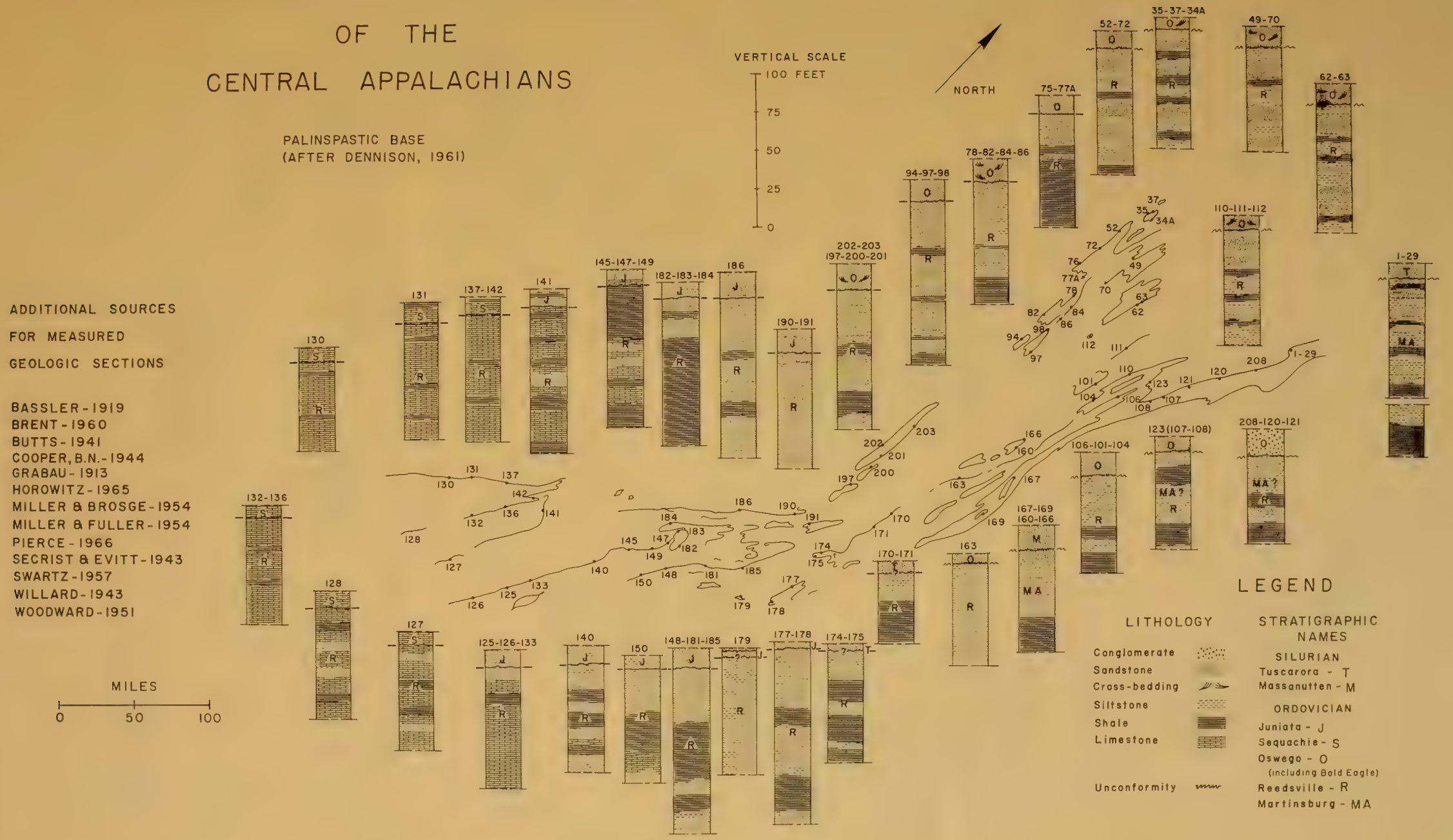

FIGURE 5.

UPPER ORDOVICIAN FAUNAL ASSOCIATIONS OF THE CENTRAL APPALACHIANS

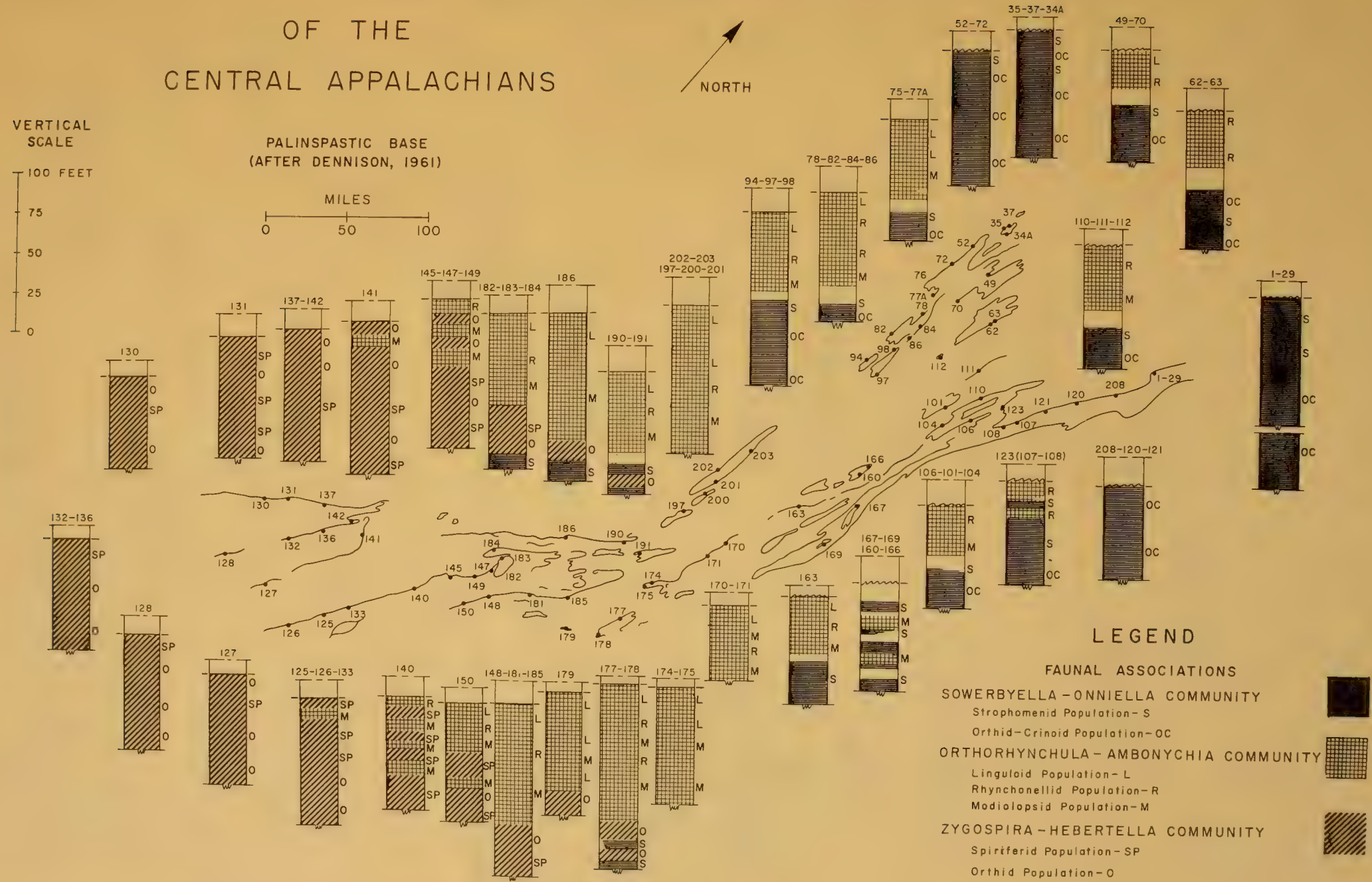

FIGURE 6.

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